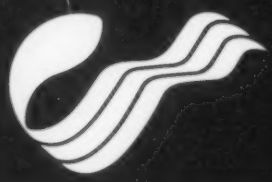


Canadian Journal of Fisheries and Aquatic Sciences

Journal canadien des sciences halieutiques et aquatiques

Fisheries and Oceans Pêches et Océans

Canada

Scientific Excellence • Resource Protection & Conservation • Benefits for Canadians

Excellence scientifique • Protection et conservation des ressources • Bénéfices aux Canadiens

The *Canadian Journal of Fisheries and Aquatic Sciences* has been published continuously since 1901, previously as *Contributions to Canadian Biology* 1901–25, *Contributions to Canadian Biology and Fisheries* 1926–34, *Journal of the Biological Board of Canada* 1934–37, and *Journal of the Fisheries Research Board of Canada* 1938–79.

Editorial Policy

The *Journal* publishes original research articles, critical reviews, perspectives (essays of opinion or hypothesis), and comments. Papers may concern cells, organisms, populations, ecosystems, or processes that affect aquatic production systems, and they should lead to identifiable conclusions or syntheses, which variously may amplify, modify, question, or redirect accumulated knowledge embodied in contemporary perceptions of a particular state of fisheries and aquatic sciences. They should demonstrate clearly a contribution to knowledge beyond the confirmation state. Originality should relate to more than the particular (a certain year, place, taxon, or chemical compound) such that existing understanding is reformulated or extended.

It would assist the Editors if prospective authors identified briefly by covering letter (a) aspects of their papers that meet the foregoing objectives, (b) potential referees, and (c) other manuscripts contemplated or in press containing the same or similar information.

Submissions in English or French are acceptable. The information must be original, that is, not copyrighted, published, or submitted elsewhere except in abstract form or unless by written consent of the Editor. The *Journal* accepts no responsibility for statements made by contributors. The use of proprietary names does not imply endorsement of the product or company.

A page charge ($44 plus 7% GST) is made for manuscripts published. When submitting a manuscript, an author must state that the charge will be accepted.

Guides

A guide for authors and typists appears in the first issue of each volume and is available free from the *Journal*.

Subscriptions

The *Journal* is issued monthly to form annual volumes of twelve numbers plus Supplements. Orders and inquiries regarding subscriptions must be sent directly to Canada Communication Group — Publishing, Supply and Services Canada, Ottawa, Ontario, Canada K1A 0S9. Prepayment is required to the order of "The Receiver General for Canada."

Microfilm

Issues from 1934 through the current volume can be purchased on 16- or 35-mm microfilm. Photocopies of individual articles or issues can be purchased from Xerox University Microfilms, 300 North Zeeb Road, Ann Arbor, Michigan 48106, USA.

Typeset and
Printed in Canada by: The Runge Press Limited, Ottawa

Composé et
Imprimé au Canada par: The Runge Press Limited, Ottawa

Design: Ludvic Saleh & Associates, Ottawa

Conception graphique: Ludvic Saleh & Associates, Ottawa

Publié sans interruption depuis 1901, le *Journal canadien des sciences halieutiques et aquatiques* a paru sous plusieurs titres : *Contributions to Canadian Biology* 1901–1925, *Contributions to Canadian Biology and Fisheries* 1926–1934, *Journal of the Biological Board of Canada* 1934–1937 et *Journal de l'office des recherches sur les pêcheries du Canada* 1938–1979.

Politique de rédaction

Le *Journal* publie des articles fondés sur une recherche originale, des critiques, des essais portant sur une opinion ou une hypothèse (perspectives) et des commentaires. Les textes peuvent avoir trait aux cellules, aux organismes, aux populations, aux écosystèmes ou aux processus qui influent sur les systèmes de production aquatique. Ils doivent aboutir à des conclusions ou synthèses précises qui, de diverses façons, peuvent accroître, modifier, remettre en question ou réorienter le bagage actuel des connaissances et perceptions dans une discipline donnée des sciences aquatiques. Ils doivent clairement démontrer qu'ils contribuent aux connaissances en faisant plus que corroborer des faits. L'originalité doit dépasser le caractère particulier (une année, un endroit, un taxon ou un composé chimique donné) et tenir à une épuration ou à une reformulation des connaissances actuelles.

Les auteurs éventuels aideraient les rédacteurs s'ils identifiaient brièvement, dans une lettre d'accompagnement a) les aspects de leurs textes qui répondent particulièrement aux objectifs indiqués ci-dessus, b) des arbitres possibles et c) d'autres manuscrits envisagés ou sous presse, dont la teneur est identique ou se rapproche de celui qui est soumis.

Les contributions peuvent être en anglais ou en français. Elles doivent être originales, c.-à-d. qu'elles ne doivent pas avoir fait l'objet d'un copyright, avoir été publiées ou soumises ailleurs, sauf sous forme abrégée ou avec le consentement du rédacteur. Le *Journal* décline toute responsabilité quant aux énoncés des contributeurs. L'utilisation des noms de marques de commerce ne signifie aucunement une sanction du produit en question ou de la compagnie qui le fabrique.

Les manuscrits acceptés sont sujets à des frais de publication (44 $ plus 7% TPS). Quand un auteur présente un texte, il doit préciser que ces frais seront acceptés. On trouvera dans une récente livraison du *Journal* les taux par page en vigueur.

Guides

Le guide des auteurs et des secrétaires d'auteurs paraît dans la première livraison de chaque volume et est offert gratuitement par le *Journal*.

Abonnement

Le *Journal* paraît tous les mois, formant ainsi un volume de douze numéros, et offre en plus jusqu'à deux suppléments par année. On doit faire parvenir les commandes et demandes de renseignements concernant les abonnements au Groupe Communication Canada — Édition, pprovisionnements et Services Canada, Ottawa (Ontario), Canada K1A 0S9. Les paiements doivent être faits à l'avance à l'ordre du Receveur général du Canada.

Microfilms

On peut acheter sur microfilms de 16 ou 35 mm tous les numéros publiés depuis 1934. Des photocopies d'articles ou de numéros individuels sont aussi en vente auprès de Xerox University Microfilms, 300 North Zeeb Road, Ann Arbor, Michigan 48106, É.-U.

Canadian Journal of Fisheries and Aquatic Sciences

Journal canadien des sciences halieutiques et aquatiques

Volume 48, No. 8, August 1991 | **Volume 48, nº 8, août 1991**

Scientific Publications/Publications scientifiques

D. G. Cook, Ph.D. — *Editor/Rédacteur*
J. Camp/G. J. Neville/P. M. Burke/M. Milne — *Editorial and Publishing Services/Services de rédaction et d'édition*
P. E. K. Symons, Ph.D. — *Consulting Editor/Rédacteur-conseil (Victoria, B.C.)*

Associate Editors/Rédacteurs associés

J. R. M. Kelso, Ph.D. — *Department of Fisheries and Oceans, Sault Ste. Marie*
C. D. Levings, Ph.D. — *Department of Fisheries and Oceans, West Vancouver*
J. D. Neilson, Ph.D. — *Department of Fisheries and Oceans, St. Andrews*
P. Schwinghamer, Ph.D. — *Department of Fisheries and Oceans, St. John's*
N. H. F. Watson, Ph.D. — *Department of Fisheries and Oceans, Halifax*
D. J. Noakes, Ph.D. — *Department of Fisheries and Oceans, Nanaimo*

Editorial Board/Conseil de rédaction

S. J. Smith — *Department of Fisheries and Oceans, Dartmouth* (1988–1991)
J. C. Roff — *University of Guelph* (1990–1992)
L. M. Dickie — *Department of Fisheries and Oceans, Dartmouth* (1990–1992)

Editorial Office:

Department of Fisheries and Oceans
Communications Directorate
Scientific Publications
200 Kent Street, 14th Floor
Ottawa, Canada K1A 0E6
Telephone (613) 993–2209
FAX (613) 990-1866

Bureau de rédaction :

Ministère des Pêches et des Océans
Direction générale des communications
Publications scientifiques
200, rue Kent, 14e étage
Ottawa, Canada K1A 0E6
Numéro de téléphone (613) 993–2209
FAX (613) 990-1866

The *Journal* is abstracted or indexed in:/Le *Journal* est résumé ou signalé dans :

Aquatic Sciences and Fisheries Abstracts, Biological Abstracts, Chemical Abstracts, Current Awareness in Biological Sciences, Current Contents, FAO Freshwater and Aquaculture Contents Tables, FAO Marine Science Contents Tables, Oceanic Abstracts, and Science Citation Index

Predicting Recruitment Variation from Year Class Specific Vertebral Counts: An Analysis of the Potential and a Plan for Verification

Kenneth T. Frank

Department of Fisheries and Oceans, Marine Fish Division, Bedford Institute of Oceanography, P.O. Box 1006, Dartmouth, N.S. B2Y 4A2, Canada

Frank, K. T. 1991. Predicting recruitment variation from year class specific vertebral counts: an analysis of the potential and a plan for verification. Can. J. Fish. Aquat. Sci. 48: 1350–1357.

Recruitment prediction has been an elusive and seemingly unobtainable goal with no entirely satisfactory general approach yet available. I propose the use of meristic variation, traditionally applied to problems associated with stock discrimination studies, as a new method to predict recruitment variation. The approach is evaluated using literature data on year class strength (YCS) and year class specific average vertebral counts (VS), two apparently interrelated variables that are affected by environmental factors operating during the early life history. Three marine stocks at the southern limit of their species geographic range (Georges Bank haddock (*Melanogrammus aeglefinus*), North Sea Atlantic cod (*Gadus morhua*), and North Sea Atlantic herring (*Clupea harengus hargenus*)) and one stock at its northern limit (Pacific herring (*Clupea harengus pallasi*)) generally conformed to the prediction of a positive relationship between YCS and VS for southern stocks and a negative relationship for northern stocks. Exceptions to these patterns were found among stocks showing low temporal variability in recruitment or for stocks whose year class formation is not linked to environmental factors that establish the vertebral count of a year class. The approach adopted is consistent with the growing initiative of focusing on characteristics of the survivors of a population to provide insight into recruitment mechanisms.

La prévision du recrutement semble être un objectif virtuellement impossible à atteindre, étant donné qu'aucune approche générale satisfaisante n'a encore été élaborée. Je propose l'utilisation de la variation méristique, traditionnellement appliquée à des problèmes associés avec des études de discrimination des stocks, comme nouvelle méthode pour prévoir la variation du recrutement. Cette approche est évaluée à l'aide de données de la documentation portant sur l'effectif de la classe annuelle (ECA) et sur des numérations moyennes de vertèbres propres à une classe annuelle, deux variables apparemment interreliées qui sont influencées par des facteurs environnementaux jouant sur toute la durée de la vie. Trois stocks marins à la limite sud de leur territoire géographique (aiglefin (*Melanogrammus aeglefinus*) du banc Georges, morue de l'Atlantique (*Gadus morhua*) de la mer du nord et hareng de l'Atlantique (*Clupea harengus harengus*) de la mer du Nord) et un stock à sa limite nord (hareng du Pacifique (*Clupea harengus pallasi*)) se sont généralement comportés selon les prévisions, affichant un rapport positif entre l'ECA et les NV dans le cas des stocks du sud, et un rapport négatif dans le cas des stocks du nord. On a observé des exceptions pour ces trois profils chez les stocks qui présentaient une faible variabilité temporelle pour ce qui est du recrutement ou chez les stocks dont les caractéristiques de la classe annuelle n'est pas reliée à des facteurs environnementaux permettant de déterminer une numération de vertèbres pour cette classe annuelle. L'approche adoptée tient compte de la méthode de plus en plus utilisée qui consiste à accorder plus d'importance aux caractéristiques des survivants d'une population pour mieux comprendre leurs mécanismes de recrutement.

Received November 13, 1990
Accepted January 14, 1991
(JA797)

Reçu le 13 novembre 1990
Accepté le 14 janvier 1991

Recently, strong criticism has been levelled at the search for and/or application of environmentally based recruitment models (Walters and Collie 1988). Direct monitoring of prerecruit year classes was advocated as a tool for recruitment prediction in place of correlative and process-oriented studies. Some of the criticisms made by Walters and Collie (1988) are indeed legitimate. For example, many of the widely known recruitment models for marine fishes have failed when tested with new data (Table 1). It should be noted that these models were largely correlative and had no process-related basis.

However, prerecruit surveys have also failed, in several instances, to provide estimates of incoming recruitment (Peterman et al. 1988). Moreover, such surveys, which require broad geographic coverage and multiple gear types to achieve adequate sampling and several years of data in order to calibrate the index with independent estimates of abundance (Koeller et al. 1986), can be very costly. As noted by Walters and Collie (1988), for a long-lived species with many year classes, only extreme changes in year class strength require anticipation. Clearly, reliable index information obtained from sources other than those mentioned above would be a superior approach to the problem.

In this paper, I propose the use of meristic variation as a source of index information on year class strength. Vertebral number in fishes has been widely studied (see review in Lindsey 1988) and geographic variation in vertebral number has been analyzed extensively in connection with stock discrimination studies (see review in Ihssen et al. 1981). Consequently, a large data base already exists with which to perform an initial evaluation of the approach.

TABLE 1. Some examples of updated environmentally based recruitment models.

Original			Update	
Source	Years	Stock	Source	Result
Carruthers et al. 1951	1920–49	North Sea cod	Saville 1959	Failed
Chase 1955	1928–51	Georges Bank haddock	Grosslein and Hennemuth 1973	Failed
Nelson et al. 1977	1955–70	Atlantic menhaden	Lasker 1985	Failed
Sutcliffe 1972, 1973	1939–70	Quebec lobster	Drinkwater et al. 1991	Failed
Sheldon et al. 1982	1950–79			
Sutcliffe et al. 1977	Various years	Several shellfish and finfish stocks in Gulf of Maine	Drinkwater and Myers 1987	Failed
Sinclair et al. 1985	1928–65	Pacific mackerel	Prager and Hoenig 1989	Failed

Rationale

The influence of environmental conditions on vertebral number in fishes has been widely documented (Hempel and Blaxter 1961; see also reviews in Garside 1966; Lindsey and Arnason 1981; Lindsey 1988). While numerous modifying factors have been identified including temperature, salinity, O_2, CO_2, light intensity, and food supply (see reviews in Templeman and Pitt 1961; Johnson and Barnett 1975; Lindsey 1988), temperature appears to have the dominant effect and is the factor most widely used to explain variation in vertebral number. For example, quantitative relationships exist between the average number of vertebrae and temperature for different populations of haddock (*Melanogrammus aeglefinus*) (Clark and Vladykov 1960) and of Atlantic cod (*Gadus morhua*) (Brander 1979) in the North Atlantic. Stocks inhabiting cooler waters for spawning and larval development typically show higher vertebral means (Fig. 1A).

In addition to the spatial variation that is common in the average number of vertebrae among stocks, there also exists significant temporal variation in mean vertebral number within stocks. For instance, Clark and Vladykov (1960) collected representative numbers of several age classes of haddock on Georges Bank in the spring and fall of 1950 and observed differences in the average number of vertebrae between year classes. These differences were, in turn, strongly correlated with the temperature conditions prevailing during spawning and early larval development. Similar relationships have been demonstrated for some clupeids (see review in Templeman and Pitt 1961; Parsons 1973), cod (Brander 1979), and Japan Sea greenling (*Pleurogrammus azonus*) (Shimazaki and Kyushin 1982). Collectively, these results are consistent with the notion that meristic characters are usually fixed at or before metamorphosis and remain constant throughout the life of an individual (Johnson and Barnett 1975; Lindsey 1988).

Environmental conditions are also known to influence year class strength, and a large body of evidence suggests that year class strength is often established during the premetamorphic phase in the life history (e.g. Roff 1981). Several studies have revealed significant relationships between recruitment (or some proxy thereof) and temperature (see reviews in Shepherd et al. 1985; Frank et al. 1988; Loeng 1989). In spite of the past failures of environmentally based recruitment models (Table 1), two facts remain: positive (negative) correlations between recruitment and temperature exist among stocks near their northern (southern) limits of distribution (Fig. 1B) (Favorite and McLain 1973; Dickson et al. 1974; Bailey and Incze 1985; Drinkwater and Myers 1987) and maximum correlations occur at time lags corresponding to the year of birth (Drinkwater and Myers 1987).

Thus, we have two apparently interrelated variables, year class strength and average vertebral number for that year class, which are affected by environmental factors operating during the early life history (premetamorphosis), that have not been systematically examined together. The following predictions can be made from the information presented: (a) mean vertebral number for a year class (VS) and year class strength (YCS) should be correlated and (b) the sign of the correlation in (a) should be negative among stocks at the northern limit of their distribution and positive among stocks at the southern limit (Fig. 1C).

Strong correlations between single environmental factors and YCS are notoriously short lived. The belief is that more than one factor or life stage can be influential in any given year or that single factors may alternately influence YCS over several years. Given the broad range of environmental variables to which VS is sensitive, it is entirely possible that VS might serve as an expression of the relative success of a year class in much the same way as other growth processes are indicative of population size and/or environmental conditions. In the remainder of the paper, the hypothesis that VS can be used to predict YCS is explored.

Methods

In the analysis which follows, I relied completely on literature data and, as expected, no single reference provided data on both variables (VS and YCS) for a particular species. Inde-

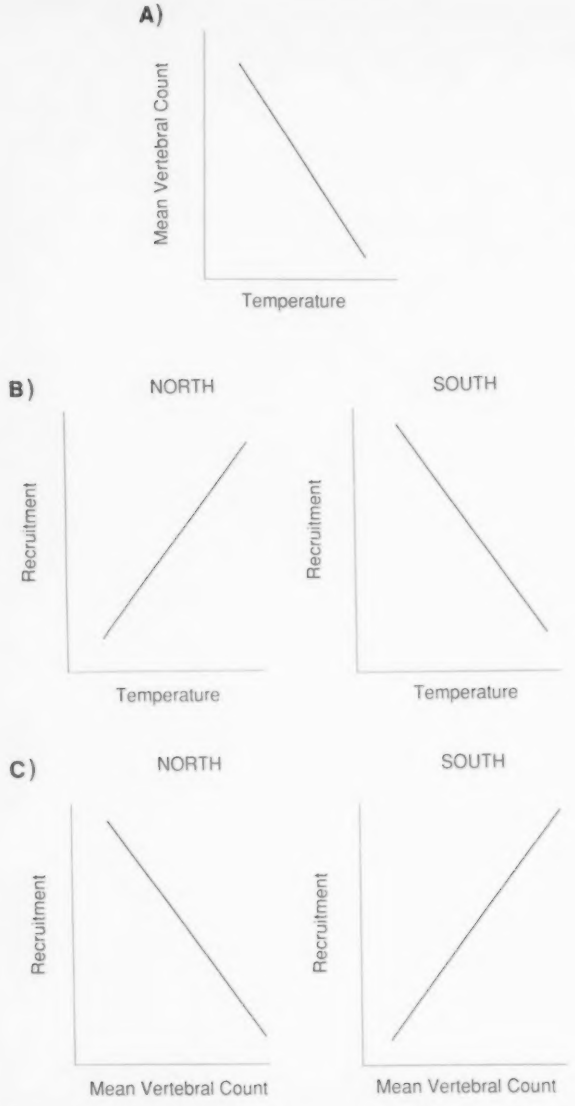


FIG. 1. (A) Generalized relationship between VS and temperature during spawning and larval development. Slope (sign of correlation) is consistent with results presented in Clark and Vladykov (1960), Brander (1979), and Scott (1972). (B) Predicted relationship between recruitment (or a proxy thereof) and temperature during the premetamorphic period for stocks at the northern limit of their species range and at the southern limit of their species range. (C) Predicted relationship between recruitment and mean vertebral count for stocks at the northern and southern limits of their species range.

pendently published data sources were, therefore, combined for each stock to test the prediction that VS and YCS are correlated and that the signs of these correlations relate to stock distributions in the manner predicted in Fig. 1.

The stocks included in the analysis were Georges Bank haddock, North Sea cod, Pacific herring (*Clupea harengus pallasi*) from Prince William Sound, Alaska, and Atlantic herring (*Clupea harengus harengus*) from the North Sea (Downs and Dogger Bank). The number of stocks ($n = 4$) available for analysis was limited either by the lack of a recruitment estimate or the lack of a mean vertebral count by year (age) class. The latter data limitation was greatest, and it has been strongly recommended that when seeking evidence of separation between stocks using vertebral counts the year class be considered (Brander 1979). Some additional stocks for which very limited data or nonoverlapping time series were available were also assessed commensurate with the hypothesis.

Results

Georges Bank Haddock

Clark and Vladykov (1960) established that year classes of Georges Bank haddock exhibited VS that differed significantly (ANOVA, $F = 4.63$, $p < 0.05$) and that were inversely correlated with water temperature averaged over March (the period of peak haddock spawning on Georges Bank; Page and Frank 1989) and April (Fig. 2A; $r = -0.86$, $p < 0.01$). These authors did not rigorously determine which year classes in the series of vertebral counts differed significantly from one another but they did present data which would allow this determination. An a posteriori means test revealed that the highest (1948) and lowest (1947) VS in the time series were significantly ($p < 0.05$) different. The vertebral count mean and variance were not correlated ($r = 0.21$, $p > 0.75$, $n = 8$), nor was there any temporal correlation evident in VS ($r = 0.16$). Mean vertebral counts decreased with increasing sea surface temperature (SST) at the time of year class formation (Fig. 2A).

Estimates of YCS of haddock (age 2) on Georges Bank exist for the interval 1931–80. These are based on virtual population analysis (Clark et al. 1982). Previous studies have shown that YCS of Georges Bank haddock is influenced by large-scale changes in environmental conditions as inferred from patterns in SST. Warming trends are typically associated with decreases in YCS and vice versa (Sutcliffe et al. 1977; Koslow et al. 1987). This result is consistent with the prediction of Fig. 1, given the fact that Georges Bank haddock are located in the southern portion of their distributional range in the Northwest Atlantic.

A positive correlation ($r = 0.55$, $p < 0.25$, $n = 8$) was found between YCS and VS during 1942–49. This correlation is substantially higher than the correlation between YCS and temperature over the same period ($r = -0.13$, $n = 8$). It is noteworthy that the lowest and highest VS were associated with the second lowest and highest recruitment estimates in the time series, respectively (Fig. 2B). In addition, the sign of the correlation coefficient between YCS and VS was positive, as expected from the predicted relationships shown in Fig. 1.

North Sea Cod

Data from Brander (1979) reveal clear differences in VS of the 1963–67 year classes of North Sea cod (Fig. 3A) that were strongly and negatively correlated with water temperature ($r = -0.95$, $p < 0.01$). No variance estimates were provided.

Dickson et al. (1974) found YCS of North Sea cod to be negatively correlated with water temperatures measured in January (time of first spawning) and in April–May (the larval drift period) during the interval 1954–68. A recent analysis of an up-to-date data series for the region by Cushing (1984) using March water temperatures and YCS estimates from 1954 to 1977 yielded a correlation coefficient of -0.45. Given that

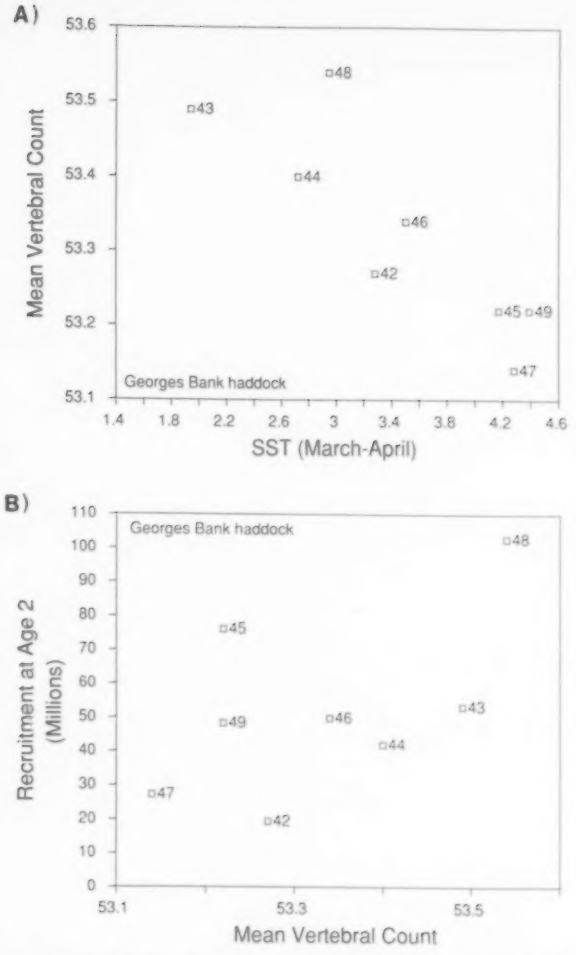


FIG. 2. (A) Relationship between VS and water temperature for the 1942–49 year classes of Georges Bank haddock (data from Clark and Vladykov 1960). (B) Relationship between recruitment for the 1942–49 year classes of Georges Bank haddock (Clark et al. 1982) and VS. Numbers next to symbols refer to birth year.

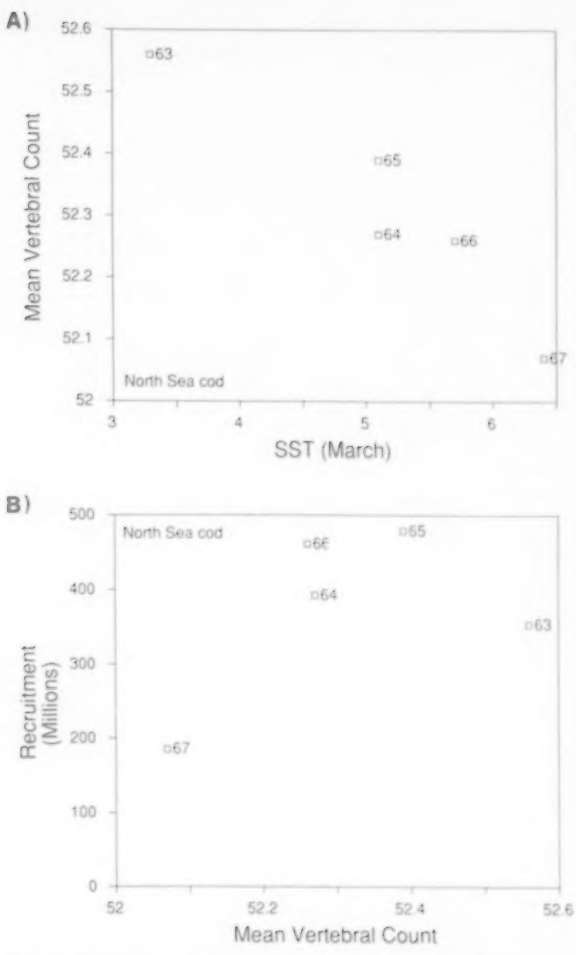


FIG. 3. (A) Relationship between VS of North Sea cod and water temperature (data from Brander 1979). (B) Relationship between cod recruitment for the 1963–67 year classes (Myers et al. 1990) and VS. Numbers next to symbols refer to birth year.

North Sea cod exist near the southern limit of the range for cod in the Northeast Atlantic, the negative correlation coefficients obtained from these analyses are consistent with the prediction of Fig. 1.

A weak positive correlation ($r = 0.51$, $n = 5$) exists between YCS (estimates obtained from Myers et al. 1990) and VS. This result was similar in several ways to that obtained for Georges Bank haddock. First, the magnitude of the correlation was greater for the relationship between YCS and VS than for YCS and water temperature. Second, the sign of the correlation between YCS and VS was positive as predicted for stocks resident in the southern portion of their species range. Finally, the lowest and highest recruitment estimates in the series were associated with the lowest and second highest VS, respectively (Fig. 3B).

Pacific Herring in Alaska

Variation in VS of the 1919–27 year classes of Prince William Sound herring was related to air temperatures averaged over the March–June postspawning period (Rounsefell and Dahlgren 1932). The correlation coefficient was -0.89 ($p < 0.01$) (Fig. 4A).

Rank estimates of herring year class strength from 1920 to 1927 revealed that strong year classes were associated with above-average air temperatures during March–June and weak year classes with below-average temperatures ($r_s = 0.71$, $p < 0.05$, $n = 8$; Rounsefell 1930). The Prince William Sound herring stock is near the northern limit of the distribution of this species in the Northwest Pacific (Hart 1973). The positive relationship between relative YCS and temperature thus conforms to the prediction of Fig. 1, although air temperature may not necessarily be a satisfactory indicator of water temperature.

Unlike the other stocks examined, the Prince William Sound herring stock was expected to show an inverse relationship between YCS and VS due to its northern position within the species range (Fig. 1C). This prediction was sustained ($r = -0.63$, $p < 0.10$, $n = 8$). The lowest and highest VS were associated with the strongest (1926) and second weakest (1920)

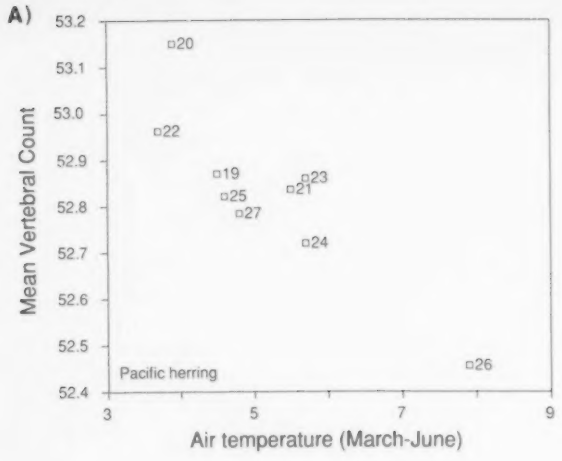


FIG. 4. (A) Relationship between VS and air temperature for the 1919–27 year classes of herring in Prince William Sound, Alaska (data from Rounsefell and Dahlgren 1932). (B) Relationship between relative YCS (strongest year class = 1) for the 1920–27 year classes of herring (Rounsefell 1930) and VS. Numbers next to symbols refer to birth year.

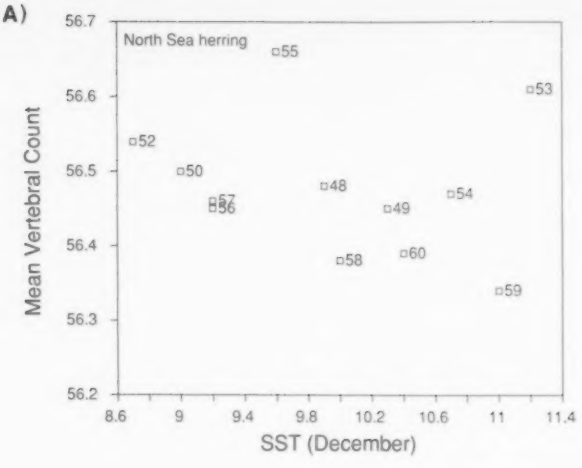


FIG. 5. (A) Relationship between VS for the "Bank" spawning stock of North Sea herring (data from Burd 1985) and water temperatures (data from Postuma 1971). (B) Relationship between North Sea herring YCS during the interval 1948–79 (data from Anonymous 1989) and VS. Numbers are year classes centred on value.

year classes in the series (Fig. 4B). This result is qualitatively similar to that obtained for haddock and cod.

North Sea Herring

For this analysis the spawning stock under consideration is referred to as the "Bank" stock and includes all herring spawning in July–October in the northern and central North Sea (Burd 1985). This stock exists near the southern limit of the range for the species in the eastern Atlantic. VS by year class are available for the period 1948–70 with occasional missing data over the period (Burd 1985). Paired vertebral count and water temperature data (from Postuma 1971) are available for a total of 13 yr. There was a weak negative correlation between VS and December water temperatures ($r = -0.20$; Fig. 5A).

YCS is generally estimated for the whole North Sea (Anonymous 1989). Postuma and Zijlstra (1974) have shown that YCS of North Sea herring is inversely related to water temperature on the spawning ground ($r = -0.50$, $n = 9$). The negative sign of the correlation coefficient is consistent with the prediction of Fig. 1, given the southern distribution of the stock.

YCS and VS were positively correlated ($r = 0.49$, $n = 27$) as predicted, although the relationship was significant ($p < 0.01$) only after logarithmic transformation of YCS (Fig. 5B). The magnitude of this correlation was equivalent to that for the YCS/temperature relationship. It should be noted, however, that the number of year classes involved in the latter relationship was one third of the former. The correlation between YCS and VS for the "Downs" spawning stock, which spawns in the southern North Sea during November to February (Burd 1985), was also positive, as expected by the current hypothesis, and was identical ($r = 0.49$, $n = 21$) to the relationship derived using the "Bank" VS.

Contrary Findings

American plaice, capelin, Flemish Cap cod

VS for the 1942–53 year classes of American plaice (*Hippoglossoides platessoides*) from St. Mary's Bay, Newfound-

land, did not vary significantly (Pitt 1963). This stock also appears to exhibit very little temporal variation in recruitment (the CV for the 1959–79 year classes of NAFO Division 3LNO plaice was 19.8%; Myers et al. 1990). Hennemuth et al. (1980) found that American plaice had the lowest CV among 18 recruitment time series evaluated. The low variance in VS is consistent with this finding.

In some stocks, environmental events associated with year class formation could be independent of those that establish the VS of a year class. Capelin (*Mallotus villotus*) may be one such example; YCS is determined both by wind events during the immediate post-hatching period and water temperatures during the period of larval drift (Leggett et al. 1984). Although the analysis considered only two year classes of capelin, Carscadden and Misra (1980) found no difference in the VS for the 1972 and 1973 year classes, which were average and strong, respectively. As noted initially, circumstances other than temperature fields and similar factors can also conspire to favour the formation of strong year classes.

Another such example may be the Flemish Cap cod stock. Akenhead (1982) has suggested that the frequency of southerly winds in March is the dominant factor influencing cod YCS in this region. Although significant temporal differences exist among the VS of cod year classes from Flemish Cap (Lear et al. 1981), they are not correlated with YCS ($r = 0.08$, $n = 10$).

Discussion

The data presented, while inadequate to fully elucidate the putative relationship between YCS and VS, are sufficiently coherent with the predictions (Fig. 1) to justify a more rigorous evaluation of the approach. It is a tantalizing possibility that year classes, particularly extreme ones, may be diagnosed from their characteristic VS. Such a pattern was evident in three of the four stocks examined.

From the data available, it is clear that the approach will not work for all species, nor should that be expected. A variety of factors may affect YCS depending upon circumstances. The best bet is for an initial evaluation of a species/population near the limits of its geographic range and for species showing high recruitment variance. As shown by Myers (1990), recruitment variance is generally greater at the northern and southern limits of a species range.

The number of stocks showing the YCS/VS correlation is sufficiently high and the form of the relationships sufficiently consistent with the predictions that careful evaluation is justified. Exactly how this would be accomplished is relatively straightforward. A directed study is advocated along the lines shown in Table 2 using, as an example, a hypothetical fish stock that is commercially exploited having 10 age groups for which population estimates at age can be made (i.e. by using sequential population analysis (SPA) techniques which reconstruct population size from catch at age data). The greater the number of ages that representative samples can be taken from for the estimation of VS the better. This will reduce the time for evaluating the approach. For the example chosen, $n = 6$ in the first year (t) of the study. This would be incremented by one each year as the preceding year class reaches age 5 and enters that portion of the population matrix considered well estimated (referred to as convergence) by SPA. Fish less than age 5 have not been in the fishery long enough to provide sufficient catch to support an accurate estimate of abundance. It is important to remember that the vertebral count for an individual is fixed at a very early age and remains constant throughout its life. It is therefore possible to estimate the vetebral count for an age class (or cohort) at any time after its formation when representative sampling can be conducted and then to establish whether significant differences in VS exist among those year classes in the time series. Following the example in Table 2 and using the variance estimates from Georges Bank haddock (Clark and Vladykov 1960), approximately 50 fish per age group would be required to detect a 1.0% difference between means 80% of the time at $p < 0.01$. Vertebral counts can be easily determined using radiographic techniques of whole fish (Bartlett and Haedrich 1966) that would subsequently be aged using scales or otoliths. Once completed, VS can be examined for its relationship to year class estimates obtained from the converged portion of the population matrix (Table 2).

TABLE 2. Population estimates (millions) for a hypothetical fishery reconstructed from catch at age data. Year t refers to the current year and VS_t is the age-specific mean vertebral count in the current year for ages 1–10. Note: only ages 5 and older would be examined for the relationship between VS and recruitment at age 1 (i.e. the bold portions of the matrix). *Year class parameter to be estimated from radiographic techniques using whole fish.

	Year										
Age	$t-9$	$t-8$	$t-7$	$t-6$	$t-5$	$t-4$	$t-3$	$t-2$	$t-1$	t	VS_t
1	**800**	**200**	**400**	**450**	**600**	**100**	420	90	10	0	*
2	268	590	120	268	350	355	70	270	65	6	*
3	50	170	440	75	180	272	210	49	171	49	*
4	124	35	110	325	45	120	212	124	35	109	*
5	165	75	25	70	240	27	80	165	73	25	*
6	55	130	43	17	45	178	16	54	129	43	*
7	10	35	100	26	12	28	132	10	36	100	*
8	95	6	25	79	15	9	18	97	6	24	*
9	16	70	4	15	61	9	6	10	73	4	*
10	15	10	50	2	10	45	5	4	7	54	*

Initially, stocks at the extremes of their species ranges, such as Georges Bank haddock or cod (southern stocks) and Northeast Arctic haddock or cod (northern stocks), would be good candidates for study, given that temporal variability in recruitment is greatest among them (Myers 1990). The approach is, of course, not just limited to marine species. If the VS of a year class is shown to be a representative index of abundance, then it could be a useful supplement to research survey abundance indices for determining the abundance of those year classes (<age 5 in our hypothetical fishery) not well estimated by SPA.

This approach may provide some quantitative insights into the question of the importance of oceanic conditions during the early life history on YCS. For example, the fact that YCS and VS tend to be more highly correlated than YCS and temperature suggests that VS reflects oceanic conditions throughout the geographical spawning and larval development region better than SST measurements at a single shore-based station. Indeed, this limitation may well be one of the principal reasons for the poor performance of some of the correlation models alluded to in Table 1, i.e. the use of environmental data from distant sources averaged over inappropriate space and time scales. If one accepts the premise that the temperature encountered by the early life stages is a good predictor of YCS for stocks at the edges of their range, then determining what that characteristic temperature is need not be a great problem. I suggest that the VS is probably a better measure of the environmental conditions encountered by the year class than some arbitrary selec-

tion of available records on temperature. Consequently, the YCS/VS correlation will provide us with a much better indication of how much of the variance in recruitment is explained by oceanic conditions operating during the early life history.

Finally, the approach developed here for predicting YCS is consistent with the growing initiative of focusing on characteristics of the survivors to provide insight into recruitment mechanisms (Rice et al. 1987; Frank and McRuer 1989), rather than elaborating possible sources of mortality for the >99% of the larvae in a cohort that typically die each year (e.g. Campana et al. 1989).

Acknowledgements

My thanks to Drs. J. E. Carscadden and W. C. Leggett for exacting criticism and encouragement on earlier drafts. Dr. S. Kerr and Mr. P. Hurley kindly commented on a second draft of this manuscript. I wish to thank the two referees (one of whom was R. H. Parrish) for their efforts and generous insights.

References

AKENHEAD, S. A. 1982. Flemish Cap cod year-class strength and environmental variables. NAFO SCR Doc. 82/VI/41. Ser. No. N530. 10 p.

ANONYMOUS. 1989. Reports of the ICES Advisory committee on fishery management, 1988. Coop. Res. Rep. No. 161.

BAILEY, K. M., AND L. S. INCZE. El Niño and the early life history and recruitment of fishes in temperate marine waters, p. 143–165. *In* W. S. Wooster and D. L. Fluharty [ed.] El Niño North: Niño effects in the eastern subarctic Pacific Ocean. Washington Sea Grant Program, University of Washington, Seattle, WA.

BARTLETT, M. R., AND R. L. HAEDRICH. 1966. Techniques in the radiography of fishes. Trans. Am. Fish. Soc. 95: 99–101.

BRANDER, K. 1979. The relationship between vertebral number and water temperature in cod. J. Cons. Int. Explor. Mer 38: 286–292.

BURD, A. C. 1985. Recent changes in the central and southern North Sea herring stocks. Can. J. Fish. Aquat. Sci. 42(Suppl. 1): 192–206.

CAMPANA, S. E., K. T. FRANK, P. C. F. HURLEY, P. A. KOELLER, F. H. PAGE, AND P. C. SMITH. 1989. Survival and abundance of young Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) as indicators of year-class strength. Can. J. Fish. Aquat. Sci. 46(Suppl. 1): 171–182.

CARRUTHERS, J. N., A. L. LAWFORD, V. F. C. VELEY, AND B. B. PARRISH. 1951. Variations in brood strength in the North Sea haddock, in the light of relevant wind conditions. Nature (Lond.) 168: 317–319.

CARSCADDEN, J. E., AND R. K. MISRA. 1980. Multivariate analysis of meristic characters of capelin (*Mallotus villosus*) in the Northwest Atlantic. Can. J. Fish. Aquat. Sci. 37: 725–729.

CHASE, J. 1955. Winds and temperatures in relation to the brood-strength of Georges Bank haddock. J. Cons. Int. Explor. Mer 21: 17–24.

CLARK, J. R., AND V. D. VLADYKOV. 1960. Definition of haddock stocks of the northwestern Atlantic. Fish. Bull. Fish Wildl. Serv. U.S. 60: 283–296.

CLARK, S. H., W. J. OVERHOLTZ, AND R. C. HENNEMUTH. 1982. Review and assessment of the Georges Bank and Gulf of Maine haddock fishery. J. Northwest Atl. Fish. Sci. 3: 1–27.

CUSHING, D. H. 1984. The gadoid outburst in the North Sea. J. Cons. Int. Explor. Mer 41: 159–166.

DICKSON, R. R., J. G. POPE, AND M. J. HOLDEN. 1974. Environmental influences on the survival of North Sea cod. p. 69–80. *In* J. H. S. Blaxter [ed.] The early life history of fish. Springer-Verlag, New York, NY. 765 p.

DRINKWATER, K. F., G. C. HARDING, W. P. VASS, AND D. GAUTHIER. 1991. The relationships of Quebec lobster landings to freshwater runoff and wind storms, p. 179–187. *In* J.-C. Therriault [ed.] The Gulf of St. Lawrence: small ocean or big estuary? Can. Spec. Publ. Fish. Aquat. Sci. 113.

DRINKWATER, K. F., AND R. A. MYERS. 1987. Testing predictions of marine fish and shellfish landings from environmental variables. Can. J. Fish. Aquat. Sci. 44: 1568–1573.

FAVORITE, F., AND D. R. MCLAIN. 1973. Coherence in transpacific movements of positive and negative anomalies of sea surface temperature, 1953–60. Nature (Lond.) 244: 139–143.

FRANK, K. T., AND J. K. MCRUER. 1989. Nutritional status of field-collected haddock (*Melanogrammus aeglefinus*) larvae from southwestern Nova Scotia: an assessment based on morphometric and vertical distribution data. Can. J. Fish. Aquat. Sci. 46(Suppl. 1): 125–133.

FRANK, K. T., R. I. PERRY, K. F. DRINKWATER, AND W. H. LEAR. 1988. Changes in the fisheries of Atlantic Canada associated with global increases in atmospheric carbon dioxide: a preliminary report. Can. Tech. Rep. Fish. Aquat. Sci. 1652: v + 52 p.

GARSIDE, E. T. 1966. Development rate and vertebral number in salmonids. J. Fish. Res. Board Can. 23: 1537–1551.

GROSSLEIN, M. D., AND R. C. HENNEMUTH. 1973. Spawning stock and other factors related to recruitment of haddock on Georges Bank. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 164: 77–88.

HART, J. L. 1973. Pacific fishes of Canada. Bull. Fish. Res. Board Can. 180: 740 p.

HEMPEL, G., AND J. H. S. BLAXTER. 1961. The experimental modification of meristic characters in herring (*Clupea harengus* L.). J. Cons. 26: 336–346.

HENNEMUTH, R. C., J. E. PALMER, AND B. E. BROWN. 1980. A statistical description of recruitment in eighteen selected fish stocks. J. Northwest Atl. Fish. Sci. 1: 101–111.

IHSSEN, P. E., H. E. BOOKE, J. M. CASSELMAN, J. M. MCGLADE, N. R. PAYNE, AND F. M. UTTER. 1981. Stock identification: materials and methods. Can. J. Fish. Aquat. Sci. 38: 1838–1855.

JOHNSON, K. J., AND M. A. BARNETT. 1975. An inverse correlation between meristic characters and food supply in mid-water fishes: evidence and possible explanations. Fish. Bull. 73: 284–298.

KOELLER, P. A., P. C. F. HURLEY, P. PERLEY, AND J. D. NEILSON. 1986. Juvenile fish surveys on the Scotian Shelf: implications for year-class size assessments. J. Cons. Int. Explor. Mer 43: 59–76.

KOSLOW, J. A., K. R. THOMPSON, AND W. SILVERT. 1987. Recruitment to northwest Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) stocks: influence of stock size and climate. Can. J. Fish. Aquat. Sci. 44: 26–39.

LASKER, R. 1985. What limits clupeoid production? Can. J. Fish. Aquat. Sci. 42(Suppl. 1): 31–38.

LEAR, W. H., R. WELLS, AND W. TEMPLEMAN. 1981. Variation in vertebral averages for year-classes of Atlantic cod, *Gadus morhua*, on Flemish Cap. J. Northwest Atl. Fish. Sci. 2: 57–60.

LEGGETT, W. C., K. T. FRANK, AND J. E. CARSCADDEN. 1984. Meteorological and hydrographic regulation of year-class strength in capelin (*Mallotus villosus*). Can. J. Fish. Aquat. Sci. 41: 1193–1201.

LINDSEY, C. C. 1988. Factors controlling meristic variation, p. 197–204. *In* W. S. Hoar and D. J. Randall [ed.] Fish physiology. Vol. XIB. Academic Press, Toronto, Ont.

LINDSEY, C. C., AND A. N. ARNASON. 1981. A model for responses of vertebral numbers in fish to environmental influences during development. Can. J. Fish. Aquat. Sci. 38: 334–347.

LOENG, H. 1989. The influence of temperature on some fish population parameters in the Barents Sea. J. Northwest Atl. Fish. Sci. 9: 103–113.

MYERS, R. A. 1990. Population variability and the range of a species. NAFO SCR Doc. 90/101. Ser. No. N1836. 8 p.

MYERS, R. A., W. BLANCHARD, AND K. R. THOMPSON. 1990. Summary of North Atlantic fish recruitment. Can. Tech. Rep. Fish. Aquat. Sci. 1743: iii + 108 p.

NELSON, W. R., M. C. INGHAM, AND W. E. SCHAAF. 1977. Larval transport and year-class strength of Atlantic menhaden, *Brevoortia tyrannus*. Fish. Bull. 75: 23–41.

PAGE, F. H., AND K. T. FRANK. 1989. Spawning time and egg stage duration in Northwest Atlantic haddock (*Melanogrammus aeglefinus*) stocks with emphasis on Georges and Browns Bank. Can. J. Fish. Aquat. Sci. 46(Suppl. 1): 68–81.

PARSONS, L. S. 1973. Meristic characteristics of Atlantic herring *Clupea harengus harengus* L. stocks in Newfoundland and adjacent waters. ICNAF Res. Bull. 10: 37–52.

PETERMAN, R. M., M. J. BRADFORD, N. C. H. LO, AND R. D. METHOT. 1988. Contribution of early life stages to interannual variability in recruitment of northern anchovy (*Engraulis mordax*). Can. J. Fish. Aquat. Sci. 45: 8–16.

PITT, T. K. 1963. Vertebral numbers of American plaice, *Hippoglossoides platessoides* (Fabricius), in the northwest Atlantic. J. Fish. Res. Board Can. 20: 1159–1178.

POSTUMA, K. H. 1971. The effect of temperature in the spawning and nursery areas on recruitment of autumn-spawning herring in the North Sea. Rapp. P.-V. Réun. Cons. Perm. Int. Explor. Mer 160: 87–93.

POSTUMA, K. H., AND J. J. ZIJLSTRA. 1974. Larval abundance in relation to stock size, spawning potential and recruitment in North Sea herring,

p. 113–128. *In* J. H. S. Blaxter [ed.] The early life history of fish. Springer-Verlag, New York, NY. 765 p.

PRAGER, M. H., AND J. M. HOENIG. 1989. Superposed epoch analysis: a randomization test of environmental effects on recruitment with application to chub mackerel. Trans. Am. Fish. Soc. 118: 608–618.

RICE, J. A., L. B. CROWDER, AND M. E. HOLEY. 1987. Exploration of mechanisms regulating larval survival in Lake Michigan bloater: a recruitment analysis based on characteristics of individual larvae. Trans. Am. Fish. Soc. 116: 703–718.

ROFF, D. A. 1981. Reproductive uncertainty and the evolution of iteroparity: why don't flatfish put all their eggs in one basket. Can. J. Fish. Aquat. Sci. 38: 968–977.

ROUNSEFELL, G. A. 1930. The existence and causes of dominant year-classes in the Alaska herring, p. 260–270. *In* Contributions to marine biology. Stanford University, Stanford, CA.

ROUNSEFELL, G. A., AND E. H. DAHLGREN. 1932. Fluctuations in the supply of herring, *Clupea pallasii*, in Prince William Sound, Alaska. Bull. U.S. Bur. Fish. 47: 262–291.

SAVILLE, A. 1959. The planktonic stages of the haddock in Scottish waters. Scott. Home Dep. Mar. Res. 1959, No. 3.

SCOTT, J. S. 1972. Morphological and meristic variation in northwest Atlantic sand lances (*Ammodytes*). J. Fish. Res. Broad Can. 29: 1673–1678.

SHELDON, R. W., W. H. SUTCLIFFE, JR., AND K. DRINKWATER. 1982. Fish production in multispecies fisheries, p. 28–34. *In* M. C. Mercer [ed.] Multispecies approaches to fisheries management advice. Can. Spec. Publ. Fish. Aquat. Sci. 59.

SHEPHERD, J. G., J. G. POPE, AND R. D. COUSENS. 1985. Variations in fish stocks and hypotheses concerning their links with climate. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 185: 255–267.

SHIMAZAKI, K., AND K. KYUSHIN. 1982. On the population of the young Japan Sea greenling, *Pleurogrammus azonus* Jordan and Metz, in the Okhotsk Sea. Bull. Fac. Fish. Hokkaido Univ. Ser VI 33: 229–239.

SINCLAIR, M., M. J. TREMBLAY, AND P. BERNAL. 1985. El Niño events and variability in a Pacific mackerel (*Scomber japonicus*) survival index: support for Hjort's second hypothesis. Can. J. Fish. Aquat. Sci. 42: 602–608.

SUTCLIFFE, W. H. JR. 1972. Some relations of land drainage, nutrients, particulate material, and fish catch in two eastern Canadian bays. J. Fish. Res. Board Can. 21: 661–680.

1973. Correlations between seasonal river discharge and local landings of American lobster (*Homarus americanus*) and Atlantic halibut (*Hippoglossus hippoglossus*) in the Gulf of St. Lawrence. J. Fish. Res. Board Can. 30: 856–859.

SUTCLIFFE, W. H. JR., K. DRINKWATER, AND B. S. MUIR. 1977. Correlations of fish catch and environmental factors in the Gulf of Maine. J. Fish. Res. Board Can. 34: 19–30.

TEMPLEMAN, W., AND T. K. PITT. 1961. Vertebral numbers of redfish, *Sebastes marinus* (L.), in the north-west Atlantic, 1947–1954. ICNAF Spec. Publ. 3: 56–89.

WALTERS, C. J., AND J. S. COLLIE. 1988. Is research on environmental factors useful to fisheries management? Can. J. Fish. Aquat. Sci. 45: 1848–1854.

Density Dependence of Larval Growth of a Marine Fish, the Southern Bluefin Tuna, *Thunnus maccoyii*

Greg P. Jenkins,[1] Jock W. Young, and Tim L. O. Davis

CSIRO Division of Fisheries, Marine Laboratories, G.P.O. Box 1538, Hobart, Tasmania 7001, Australia

Jenkins, G. P., J. W. Young, and T. L. O. Davis. 1991. Density dependence of larval growth of a marine fish, the southern bluefin tuna, *Thunnus maccoyii*. Can. J. Fish. Aquat. Sci. 48: 1358–1363.

Competition for food among larvae and subsequent reduction in growth rates has been proposed as a mechanism to explain the apparent density-dependent control of some exploited marine fish populations, but has received little support from field data. Growth of larvae of southern bluefin tuna, *Thunnus maccoyii*, in the East Indian Ocean was significantly different among stations sampled randomly within a 20-km radius. Growth rate was positively correlated with feeding rate but not with temperature, indicating that larvae were food limited to a varying degree. A negative correlation between growth rate and abundance suggested that food limitation was density dependent. Regression analysis indicated that in areas of highest larval densities there was an approximate 25% reduction in growth rate. We suggest that in areas of high abundance, larvae were competing for food, leading to a density-dependent reduction of growth rate. Because the larval stage of high mortality is prolonged, cumulative mortality of slow-growing larvae over this period may be greater, even if the mortality rate is constant.

La compétition alimentaire entre les larves de poissons sous-tendant une baisse des taux de croissance a été avancée comme la théorie expliquant le contrôle apparent, dépendant de la densité, de certaines populations de poissons marins exploitées. Cette théorie n'a toutefois pas été étayée par des données expérimentales. Le taux de croissance de larves de thon rouge du sud, *Thunnus maccoyii*, dans le secteur est de l'océan Indien était nettement différent entre les stations échantillonnées au hasard dans un rayon de 20 km. Il était en corrélation positive avec le taux d'alimentation, mais non avec la température; ceci révèle que les larves disposaient d'une source limitée de nourriture à divers degrés. Une corrélation négative entre le taux de croissance et l'abondance porte à croire que la quantité de nourriture disponible était liée à la densité des larves. Les résultats d'une analyse de régression indiquent que le taux de croissance était réduit de 25 % environ dans les régions de plus fortes densités de larves. Les auteurs formulent l'hypothèse que dans les régions d'abondance élevée, la compétition pour la nourriture entre les larves entraîne une baisse du taux de croissance liée à la densité. Étant donné que le stade larvaire est exposé à une longue période de mortalité, la mortalité cumulative des larves à croissance lente pendant cette période peut être plus élevée même si le taux de mortalité est constant.

Received May 17, 1990
Accepted March 8, 1991
(JA579)

Reçu le 17 mai 1990
Accepté le 8 mars 1991

The inability to understand and predict the variability of recruitment in marine fishes is the major problem confronting fisheries science and management (Sissenwine 1984). Typically, the relationship between stock and recruitment shows high variability; the effect of stock on recruitment is apparently obscured by high variability due to density-independent processes (Welch 1986). Nevertheless, it has been argued (Shepherd and Cushing 1980; Cushing 1988) that significant density- (stock-) dependent effects must operate in populations of exploited fish, where, in the face of heavy exploitation, recruitment has remained relatively constant over a long period of time.

The mechanism which has been proposed as most likely to explain the relatively strong component of density-dependent mortality in some fishes is the interaction between predation and density-dependent growth in the larval stage (Shepherd and Cushing 1980; Cushing 1988). Thus, if larvae are sufficiently abundant, food may be depleted to the point where larvae grow more slowly. Because slow growth leads to a prolonged larval stage of assumed high predation mortality, cumulative mortality over this period may be greater, even if the mortality rate is constant (Houde 1987; Bailey and Houde 1989).

Estimates of the grazing pressure exerted by larval marine fish suggest that larvae may (Bollens 1988; Kiørboe et al. 1988) or may not (Cushing 1983; Peterson and Ausubel 1984; Jenkins 1987) impact prey populations. The extent to which this dichotomy is a result of differences among the species and communities examined, or even differences among the methods used to estimate grazing pressure, is not clear. If larvae impact on prey populations, intraspecific competition for food would be likely. Estimates of recent growth using biochemical (Buckley and Lough 1987; Håkanson 1989) and the otolith daily increment (Govoni et al. 1985) techniques suggest that larval growth rate may be limited by food availability in the sea. However, although the effect of competition for food on growth can be easily demonstrated in the laboratory using unnaturally high densities of larvae (Wyatt 1972; Laurence et al. 1981; Houde and Schekter 1981), field evidence linking competition for food to limitation of growth is lacking.

The only known spawning area for southern bluefin tuna, *Thunnus maccoyii*, is off northwest Australia. Juveniles subsequently migrate around the southern coast of Australia, and

[1]Present address: Department of Zoology and Victorian Institute of Marine Sciences, University of Melbourne, Parkville, Victoria 3052, Australia.

when mature move off the Australian shelf and disperse throughout the Southern Ocean. The distribution is almost circumpolar between latitudes 30 and 50°S (Shingu 1980). The population is fished by Australia, Japan, New Zealand, and other countries at various stages of the life cycle; it is thought to be substantially overexploited, and the future of the population at present levels of exploitation is in doubt (Caton and Majkowski 1987).

As part of a study of the early life history of southern bluefin tuna on their spawning grounds off the northwest shelf of Australia, we investigated the possibility of density-dependent growth of larvae through competition for food. The southern bluefin tuna population is one where density-dependent population control may be expected (Shepherd and Cushing 1980) because, although the rate of exploitation is high, recruitment, at least up to 1980 which is the most recent estimate, has remained relatively constant (Caton and Majkowski 1987). Sampling was conducted in the area of a concentrated patch of *T. maccoyii* larvae, with peak densities reaching $22 \cdot m^{-3}$ (Davis et al. 1990a), the highest yet recorded for tuna larvae. On the basis of larval abundances, larval feeding rates, and prey abundances, Young and Davis (1990) have suggested that a significant reduction of prey populations would have been likely near the centre of the patch, and competition for food was therefore possible. The otoliths of *T. maccoyii* contain daily increments which can be used to back-calculate the growth rate of individual larvae (Jenkins and Davis 1990). Here we combine data on growth rates and food consumption from this patch to examine the possibility of density-dependent reduction in growth rate due to competition for food.

Methods

Sampling was carried out off the northwest of Australia from 29 January to 2 February 1987. Exploratory sampling revealed a concentration of *T. maccoyii* larvae at 16°30.2′S, 115°50.4′E, where a satellite-tracked buoy with parachute drogue set at 20 m was immediately deployed. A series of samples at positions randomly generated by computer were collected within a 20-km radius of the buoy over 5 d (Fig. 1).

Approximately 12 day and 10 night samples were taken every 24 h. Half of the stations were sampled with a 10-min double-oblique tow to the thermocline, while the remaining stations were sampled with a combination of a 10-min surface tow and a 20-min double-oblique tow to the thermocline, with nets deployed concurrently. All samples were collected with a 0.5-mm-mesh cylinder-cone net attached to a 70-cm collar. Samples were preserved in 95% ethanol, which was replaced with fresh ethanol within 24 h. Full descriptions of the net and sampling are given in Davis et al. (1990b).

Larvae collected in oblique tows were used in this study. Larvae were sorted from plankton samples in a rotatable sorting ring under a dissecting microscope with dark-field illumination. Where more than 20 larvae occurred in a sample, a random subsample of 20 larvae was examined. Standard length (SL; tip of the snout to tip of the notochord, or the hypural crease in postflexion larvae) was measured under a dissecting microscope with an ocular micrometer. SL was not corrected to live length. Otoliths and gut contents were teased out of larvae with electrolytically sharpened tungsten needles.

Stomach contents were excised in glycerine containing Chlorazol Black e to aid identification and counting. Feeding incidence (percentage of feeding larvae per sample), mean stomach fullness (a subjective rating of fullness ranging from 1 to 5: 1 = empty; 2 < half-full; 3 ≈ half-full; 4 > half-full; 5 = full), and mean prey number were determined for larvae from each sample.

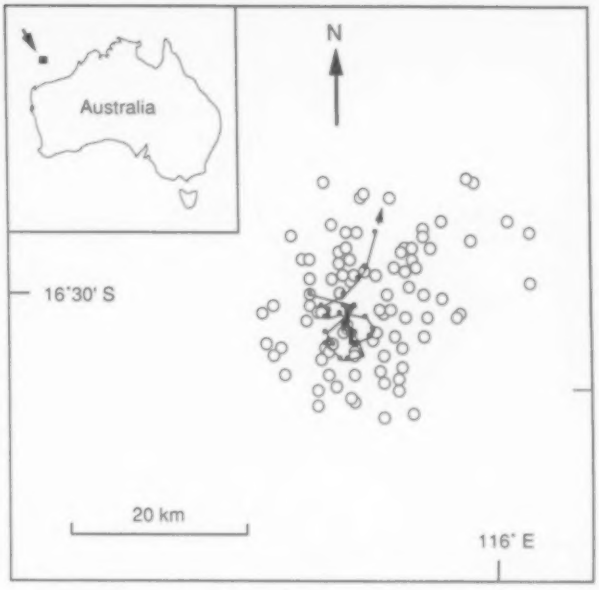


FIG. 1. Chart showing stations sampled for tuna larvae in the East Indian Ocean. The continuous line indicates track of satellite-tracked drogue; the arrow indicates the direction of movement. Inset: location of sampling area relative to the Australian coast.

Sagittae and lapilli were permanently mounted on a microscope slide with Gurr's neutral mounting medium. Otoliths were viewed with a video system fitted to a compound microscope at a magnification of 920 or 2360×. An H.E.I. "Video coordinate digitizer" and a microcomputer were used to digitize otolith counts and measurements.

A strong log-linear relationship between larval length and sagittal otolith radius ($SL = 2.613 \times \ln rad - 3.406$, $r^2 = 0.913$), together with the presence of daily growth increments, enabled us to estimate the length of each larva on each day of life by substituting the log-transformed otolith radius to each daily increment into the regression equation (Jenkins and Davis 1990). This was done for larvae from 27 stations with more than 10 larvae. Twenty of these stations were sampled on 30 and 31 January. Growth trajectories of all larvae were strongly linear ($r^2 = 0.97$ to 1.00); therefore the regression coefficient of a straight line fitted to the back-calculated sizes-at-age gave a good estimate of the growth rate averaged over the life of an individual larva. Assumptions upon which this method is based are discussed in Jenkins and Davis (1990). For parametric tests, abundances were expressed as $\log_{10}(x + 1) \cdot 1000\ m^{-3}$.

Results and Discussion

Thunnus maccoyii larvae from the 27 stations analyzed ranged from 3.4 to 7.5 mm in length and had between 4 and 13 daily increments (Table 1). The average individual growth rates at stations ranged from 0.28 to 0.37 $mm \cdot d^{-1}$ (Table 1). Individual growth rates of *T. maccoyii* larvae were significantly different amongst stations (ANOVA $F = 6.09$, df = 26/417,

$P < 0.001$). In the case of stations sampled on 30 and 31 January, growth rates varied widely over a scale of a few kilometres (Fig. 2), with a trend of increasing growth rates from east to west. There was a slight southward advection of the larval patch relative to the buoy over this 2-d period (Davis et al. 1990a); thus the true relationship between stations in space may be expected to be compressed slightly in the north–south direction.

Temperature and food availability are likely to be the most important environmental variables affecting growth rate (Methot and Kramer 1979). Mean growth rate was not significantly correlated with surface temperature (Pearson's $r = 0.30$, df $= 26$, $P > 0.1$; Fig. 3). This is not surprising because the range of temperatures was very narrow (27.25–27.70°C). This temperature should be representative of that experienced by larvae because the majority of larvae occurred in the mixed layer and temperature was relatively constant from the surface to the top of the pycnocline during this cruise (Davis et al. 1990b).

Feeding in *T. maccoyii* larvae occurred only during daytime (Young and Davis 1990); therefore, analyses involving feeding were restricted to stations sampled in daylight only. A significant difference in average individual growth rate among stations sampled in daylight was still apparent ($F = 5.41$, df $= 13/211$, $P < 0.001$). Feeding incidence (Pearson's $r = 0.69$, df $= 13$, $P < 0.01$), mean stomach fullness (Pearson's $r = 0.71$, df $= 13$, $P < 0.01$), and mean prey number (Pearson's $r = 0.64$, df $= 13$, $0.01 < P < 0.02$) all showed a significant positive correlation with mean growth rate at stations (Fig. 4).

One explanation for the significant correlation between feeding indices and growth rates is that larvae may have developed poorly, for reasons such as low parental investment (i.e. small egg size, low yolk content (Hunter 1981)), causing larvae to grow slowly and also to have a low feeding success, independent of prey concentration. However, indices of feeding in this study were significantly correlated with zooplankton volume (Young and Davis 1990), so these indices reflected the food available in the larval environment. It is most likely, therefore, that variation in larval growth rate was due to fine- to coarse-scale spatial variation in food supply.

Mean growth rate was negatively correlated with abundance of larvae at stations (Pearson's $r = -0.61$, df $= 26$, $P < 0.001$; Fig. 5), suggesting that growth rate was a density-dependent function of abundance. Two alternative explanations for this result appear less likely.

Firstly, the correlation would occur without causation if abundance were negatively correlated and growth rate were positively correlated with the same third variable, age (which approximates time because we were dealing with a single cohort). For *T. maccoyii* larvae, absolute age from fertilization is approximated by the number of daily increments plus 3 d (Jenkins and Davis 1990). As would be expected, log abundance was negatively correlated with mean number of daily increments at stations (Pearson's $r = -0.458$, df $= 26$, $0.01 < P < 0.02$; Fig. 6), presumably due to the effects of mortality and net avoidance. Hunter and Kimbrell (1980) found

TABLE 1. Mean, standard error, and range of standard length, number of increments, and back-calculated growth rate of *T. maccoyii* larvae collected between 29 January and 2 February 1987 (n = number of larvae for which growth rate was back-calculated).

		Standard length (mm)			Number of increments			Estimated growth rate ($mm \cdot d^{-1}$)		
Station	n	$\bar{X}$	SE	Range	$\bar{X}$	SE	Range	$\bar{X}$	SE	Range
252	19	4.4	0.1	3.6–5.0	7.2	0.2	6–8	0.320	0.006	0.263–0.355
253	18	4.4	0.1	4.1–5.1	6.2	0.1	6–7	0.336	0.008	0.268–0.398
267	15	3.9	0.1	3.5–4.5	6.6	0.2	6–8	0.288	0.009	0.232–0.354
268	19	4.4	0.2	3.6–5.9	6.9	0.4	5–11	0.341	0.009	0.285–0.452
271	11	4.9	0.1	4.2–5.7	8.5	0.3	7–10	0.360	0.016	0.301–0.433
272	18	4.4	0.1	3.6–4.9	6.8	0.2	6–8	0.311	0.009	0.232–0.383
273	13	5.1	0.3	3.6–6.6	8.2	0.4	5–11	0.363	0.011	0.300–0.448
274	18	4.6	0.1	3.8–5.3	7.6	0.1	7–9	0.310	0.009	0.223–0.359
276	18	4.0	0.1	3.6–4.7	6.7	0.2	5–8	0.300	0.009	0.245–0.392
277	18	4.1	0.1	3.6–5.2	6.9	0.3	6–10	0.344	0.009	0.279–0.409
280	17	4.5	0.1	3.8–5.8	7.8	0.2	7–10	0.333	0.013	0.259–0.416
284	15	4.3	0.1	3.4–5.2	7.4	0.4	4–10	0.293	0.016	0.211–0.406
289	15	4.4	0.1	4.2–5.2	7.5	0.2	7–9	0.322	0.006	0.275–0.351
290	17	4.7	0.2	3.9–7.5	7.7	0.3	6–11	0.313	0.013	0.233–0.465
291	15	4.3	0.1	4.0–5.0	7.3	0.2	7–9	0.306	0.009	0.259–0.350
294	12	5.0	0.1	4.3–5.5	8.3	0.2	7–10	0.339	0.013	0.246–0.418
298	15	5.1	0.2	4.2–6.7	8.5	0.3	7–11	0.338	0.010	0.277–0.408
299	17	4.4	0.1	4.1–4.9	8.2	0.2	6–9	0.299	0.010	0.242–0.373
300	18	4.5	0.1	3.7–5.2	8.6	0.1	8–9	0.291	0.011	0.202–0.422
303	17	5.0	0.1	4.1–5.8	8.1	0.2	7–9	0.356	0.009	0.250–0.408
304	18	4.7	0.1	4.2–6.1	8.4	0.2	7–11	0.330	0.009	0.246–0.391
306	20	5.1	0.2	4.1–6.7	8.7	0.3	7–12	0.367	0.006	0.312–0.407
310	18	4.6	0.1	4.0–5.5	8.8	0.1	8–9	0.278	0.013	0.208–0.407
311	17	5.1	0.2	4.1–6.5	9.1	0.3	8–13	0.282	0.009	0.226–0.347
326	12	5.0	0.1	4.3–5.8	9.2	0.1	9–10	0.348	0.120	0.289–0.416
342	18	5.2	0.1	4.5–6.2	10.4	0.2	8–12	0.299	0.010	0.232–0.364
343	16	5.2	0.2	4.2–6.2	10.4	0.3	8–12	0.308	0.017	0.220–0.456

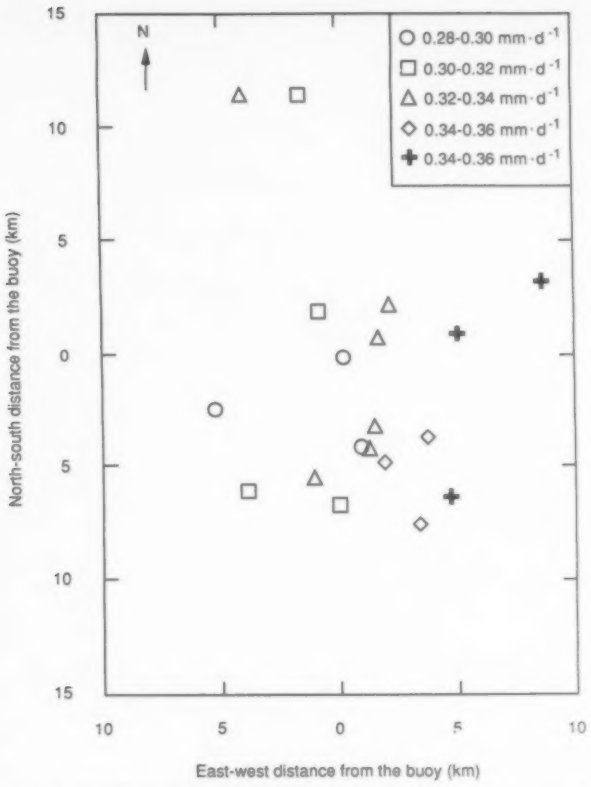


FIG. 2. Distribution of mean individual growth rates of *T. maccoyii* larvae from random stations sampled on 30 and 31 January 1987.

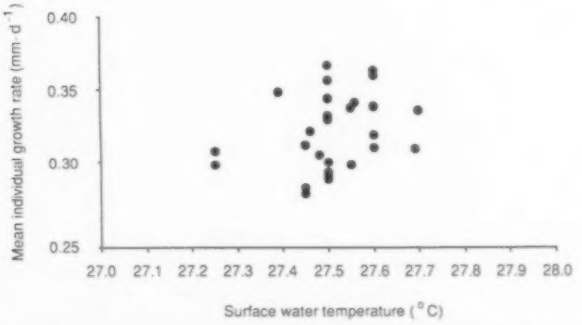


FIG. 3. Relationship between mean individual growth rate and surface temperature for *T. maccoyii* larvae at random stations.

that older larvae of the scombrid *Scomber japonicus* grew faster than younger ones in the laboratory. However, for *T. maccoyii* larvae in the present study, there was no significant correlation between mean individual growth rates and the mean number of daily increments at stations (Pearson's $r = -0.045$, df = 26, $0.8 < P < 1.0$; Fig. 7). A more powerful test for a relationship between growth rate and age was to use individual growth rates and increment numbers rather than station means. However, once again, no significant relationship was found (Pearson's $r = 0.057$, df = 443, $0.2 < P < 0.5$). Late-stage larvae, collected away from the major larval patch and not

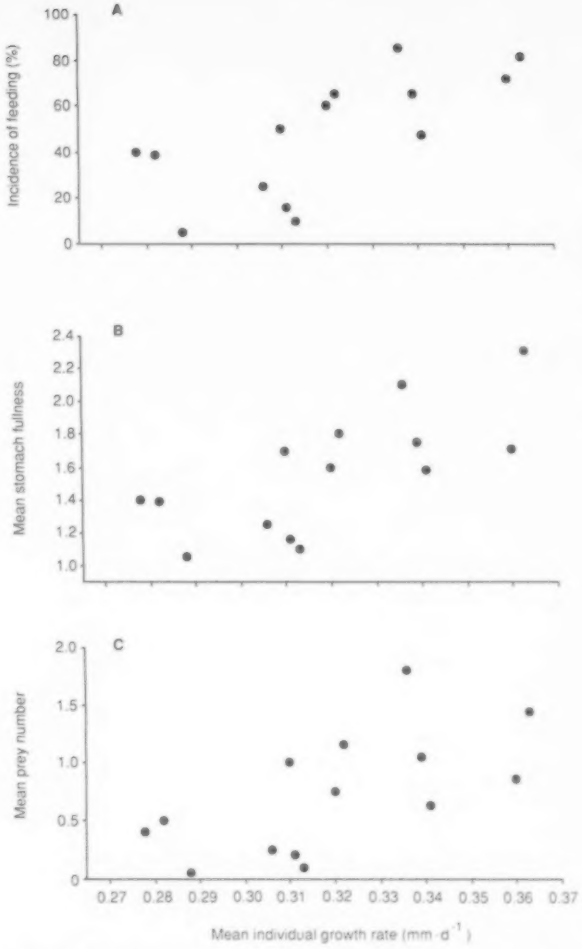


FIG. 4. Relationship between mean individual growth rate and (A) feeding incidence, (B) mean stomach fullness, and (C) mean prey number for *T. maccoyii* larvae at random stations sampled in daylight.

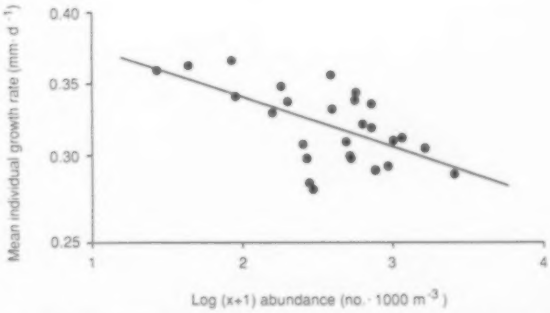


FIG. 5. Relationship between mean individual growth rate and log abundance for *T. maccoyii* larvae at random stations. The line represents the linear regression of mean individual growth rate on log abundance (slope = −0.034, intercept = 0.41, $r^2 = 0.367$).

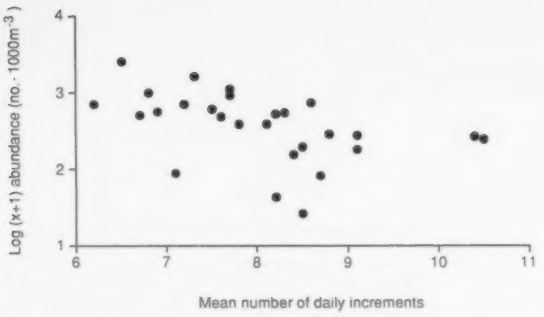


FIG. 6. Relationship between mean number of daily increments and log abundance for *T. maccoyii* larvae at random stations.

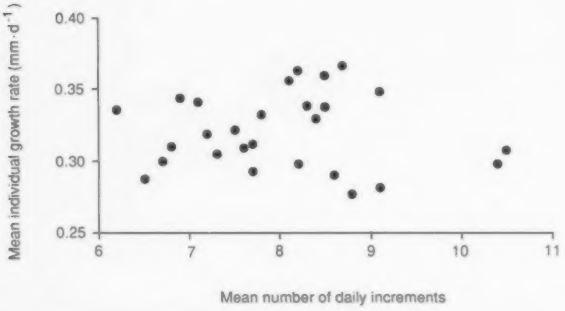


FIG. 7. Relationship between mean number of daily increments and mean individual growth rate for *T. maccoyii* larvae at random stations.

included in the samples examined here, showed positive curvilinearity in later larval life (Jenkins and Davis 1990). In contrast, some older larvae collected within the larval patch showed a tendency towards negative curvilinearity (Jenkins and Davis 1990). It is probable that the growth of older *T. maccoyii* larvae does show positive curvilinearity when food is plentiful, but in the larval patch studied here, there was no relationship between growth rate and age.

Secondly, if slow-growing larvae were more susceptible to capture because of poor condition, more larvae would be collected in areas of slow growth. However, laboratory experiments on larvae of a number of species have shown that nutritional effects on vulnerability are not significant unless starvation is inevitable (beyond the point of no return (PNR)), when 50% of larvae are two weak to feed) (Yin and Blaxter 1987). Amongst the slowest growing larvae in the present study were older larvae which had grown at a constant slow rate; these larvae were obtaining enough food to prevent starvation, and therefore, their escape response should not have been inhibited. In fact, Yin and Blaxter (1987) found that response rates and escape speeds actually tended to peak 1–2 d before the PNR. The major factor producing the two-order magnitude of variation in abundance was patchy spawning of adults (Davis et al. 1990a); therefore, variation in numbers due to escape ability would have been relatively insignificant.

A simple calculation can illustrate the potential for density-dependent reduction in growth rate to generate recruitment variability in *T. maccoyii*. A linear regression model was used to relate growth rate to log abundance (Fig. 5). An intercept of 0.41 mm·d^{-1} indicates that at stations with lowest densities, there might have been a near negligible effect of density on growth rate. This suggests that in areas of highest larval densities, there was an approximate 25% density-dependent reduction in growth rate. The larval stage in *T. maccoyii* lasts approximately 20 d (Jenkins and Davis 1990). If a 20-d larval period is assumed for larvae unaffected by density-dependent reduction in growth rate, then larvae from high-density areas will have a 25-d duration of the larval period. The total mortality rate operating at the time of sampling was approximately $z = 0.66 \cdot d^{-1}$ (50%·d^{-1}) (Davis et al. 1991). If this rate were constant over the larval period, then there would be a 27-fold difference in the number surviving the end of the larval period.

It is apparent from the results presented here, together with previous evidence that *T. maccoyii* larvae had the potential to significantly reduce prey populations in the sampling area (Young and Davis 1990), that larvae occurring in high concentrations were competing for prey and a significant reduction in growth rate resulted. This result is in contrast with results for jack mackerel, *Trachurus symmetricus*, where growth rate was not significantly different between areas of high and low density, suggesting no density-dependent effect on growth (Hewitt et al. 1985).

We are unsure of the overall importance of density-dependent larval mortality to the population dynamics of *T. maccoyii*. Abundances of *T. maccoyii* larvae were high compared with those recorded in previous larval tuna surveys; however, this was probably more a function of inappropriate sampling scales in previous studies rather than real differences (Davis et al. 1990a). More information is required on the distribution and intensity of larval *T. maccoyii* patches over the spatial and temporal range of spawning. The magnitude of the compensatory effect of density-dependent larval growth as the reproductive population is reduced by fishing would depend on whether spawning fish respond to population decline by forming smaller spawning aggregations, or fewer spawning aggregations of a constant size. No information is presently available to support either of these possible responses.

Competition for food amongst fish larvae and subsequent density-dependent growth may be more likely in environments such as the oligotrophic waters of the East Indian Ocean (Rochford 1962) where prey abundances are low. Studies where grazing pressure exerted by larval fish was considered to be insignificant have all concentrated on relatively productive, nearshore waters (Cushing 1983; Peterson and Ausubel 1984; Jenkins 1987).

The finding that juveniles of *Thunnus thynnus* were derived from fast-growing larvae (Brothers et al. 1983) lends support to the contention that faster growing larvae have a higher probability of survival. Older larvae of *T. maccoyii*, which are size-selective predators, consume their smaller siblings (Young and Davis 1990). Cannibalism may be a source of density-dependent mortality in its own right (Smith 1985), but its effect may be compounded if young larvae are competing for food and growth rates are reduced.

Unfortunately, the age range of *T. maccoyii* larvae in samples was too narrow to directly test for density-dependent mortality. Significant density-dependent mortality in the egg and larval stage has been demonstrated for the anadromous shad *Alosa sapidissima* (Savoy and Crecco 1988); however, the mechanisms which produce density dependence in a riverine environment may be quite different from that proposed here.

In summary, we have provided field evidence for density-dependent control of larval growth through competition for food

which has been hypothesized to explain the density-dependent population regulation which must occur in some marine fishes. Most research into the larval phase of marine fishes has emphasized density-independent processes. Our results show that density-dependent processes may also play a role in determining recruitment success of marine fishes.

Acknowledgements

We thank the Master and crew of the FRV *Soela* for their assistance with fieldwork. We thank P. Bonham, O. Augustine, and J. May for sorting samples and P. Bonham for identifying larvae. G. Harris, W. Kimmerer, R. Johannes, V. Mawson, and F. R. Harden Jones made many useful suggestions for improving the manuscript. This work was carried out while the senior author was the recipient of a CSIRO Postdoctoral Award.

References

BAILEY, K. M., AND E. D. HOUDE. 1989. Predation on eggs and larvae of marine fishes and the recruitment problem. Adv. Mar. Biol. 25: 1–83.

BOLLENS, S. M. 1988. A model of the predatory impact of larval marine fish on the population dynamics of their zooplankton prey. J. Plankton Res. 10: 887–906.

BROTHERS, E. B., E. D. PRINCE, AND D. W. LEE. 1983. Age and growth of young-of-the-year bluefin tuna, *Thunnus thynnus*, from otolith microstructure. NOAA Tech. Rep. NMFS 8: 49–59.

BUCKLEY, L. J., AND R. G. LOUGH. 1987. Recent growth, biochemical composition and prey field of larval haddock (*Melanogrammus aeglefinus*) and Atlantic cod (*Gadus morhua*) on Georges Bank. Can. J. Fish. Aquat. Sci. 44: 14–25.

CATON, A., AND J. MAJKOWSKI. 1987. Warning issued on global catch limits. Aust. Fish. 46: 22–24.

CUSHING, D. H. 1983. Are fish larvae too dilute to affect the density of their food organisms? J. Plankton Res. 5: 847–854.

1988. The study of stock and recruitment, p. 105–128. *In* J. A. Gulland [ed.] Fish population dynamics (second edition). John Wiley & Sons, London.

DAVIS, T. L. O., G. P. JENKINS, AND J. W. YOUNG. 1990a. Patterns of horizontal distribution of the larvae of southern bluefin (*Thunnus maccoyii*), and other tuna in the Indian Ocean. J. Plankton Res. 12: 1295–1314.

1990b. Diel patterns of vertical distribution in larvae of southern bluefin *Thunnus maccoyii* and other tuna in the East Indian Ocean. Mar. Ecol. Prog. Ser. 59: 63–74.

DAVIS, T. L. O., V. LYNE, AND G. P. JENKINS. 1991. Advection, dispersion and mortality of a patch of southern bluefin tuna larvae (*Thunnus maccoyii*) in the East Indian Ocean. Mar. Ecol. Prog. Ser. (In press)

GOVONI, J. J., A. J. CHESTER, D. E. HOSS, AND P. B. ORTNER. 1985. An observation of episodic feeding and growth of larval *Leiostomus xanthurus* in the Northern Gulf of Mexico. J. Plankton Res. 7: 137–146.

HÅKANSON, J. L. 1989. Condition of larval anchovy (*Engraulis mordax*) in the Southern California Bight, as measured through lipid analysis. Mar. Biol. 102: 153–159.

HEWITT, R. P., G. H. THEILACKER, AND N. C. H. LO. 1985. Causes of mortality in young jack mackerel. Mar. Ecol. Prog. Ser. 26: 1–10.

HOUDE, E. D. 1987. Fish early life dynamics and recruitment variability. Am. Fish. Soc. Symp. No. 2: 17–29.

HOUDE, E. D., AND R. C. SCHEKTER. 1981. Growth rates, rations and cohort consumption of marine fish larvae in relation to prey concentrations. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 178: 441–453.

HUNTER, J. R. 1981. Feeding ecology and predation of marine fish larvae, p. 33–77. *In* R. Lasker [ed.] Marine fish larvae. Morphology, ecology and relation to fisheries. Washington Sea Grant Program, Seattle and London.

HUNTER, J. R., AND C. A. KIMBRELL. 1980. Early life history of Pacific mackerel, *Scomber japonicus*. Fish. Bull. U.S. 78: 89–101.

JENKINS, G. P. 1987. Comparative diets, prey selection and predatory impact of co-occurring larvae of two flounder species. J. Exp. Mar. Biol. Ecol. 110: 147–170.

JENKINS, G. P., AND T. L. O. DAVIS. 1990. Age, growth rate, and growth trajectory determined from otolith microstructure of southern bluefin tuna *Thunnus maccoyii* larvae. Mar. Ecol. Prog. Ser. 63: 93–104.

KIØRBOE, T., P. MUNK, K. RICHARDSON, V. CHRISTENSEN, AND H. PAULSEN. 1988. Plankton dynamics and larval herring growth, drift and survival in a frontal area. Mar. Ecol. Prog. Ser. 44: 205–219.

LAURENCE, G. C., A. S. SMIGIELSKI, T. A. HALAVIK, AND B. R. BURNS. 1981. Implications of direct competition between larval cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) in laboratory growth and survival studies at different food densities. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 178: 304–311.

METHOT, R. D. JR., AND D. KRAMER. 1979. Growth of northern anchovy, *Engraulis mordax*, larvae in the sea. Fish. Bull U.S. 77: 413–423.

PETERSON, W. T., AND S. L. AUSUBEL. 1984. Diets and selective feeding by larvae of Atlantic mackerel *Scomber scombrus* on zooplankton. Mar. Ecol. Prog. Ser. 17: 65–75.

ROCHFORD, D. J. 1962. Hydrology of the Indian Ocean. Part II: the surface waters of the southeast Indian Ocean and the Arafura Sea in the spring and summer. Aust. J. Mar. Freshwater Res. 13: 226–251.

SAVOY, T. F., AND V. A. CRECCO. 1988. The timing and significance of density-dependent and density-independent mortality of American shad, *Alosa sapidissima*. Fish. Bull. U.S. 86: 467–482.

SHEPHERD, J. G., AND D. H. CUSHING. 1980. A mechanism for density-dependent survival of larval fish as the basis of a stock–recruitment relationship. J. Cons. Int. Explor. Mer 39: 160–167.

SHINGU, C. 1980. Ecology and stock of southern bluefin tuna. Tech. Rep. Div. Fish. Oceanogr. C.S.I.R.O. 131: 1–79.

SISSENWINE, M. P. 1984. Why do fish populations vary?, p. 59–94. *In* R. May [ed.] Exploitation of marine communities. Springer-Verlag, Berlin.

SMITH, P. E. 1985. Year-class strength and survival of O-group clupeoids. Can. J. Fish. Aquat. Sci. 42(Suppl. 1): 69–82.

WELCH, D. W. 1986. Identifying the stock–recruitment relationship for age-structured populations using time-invariant matched linear filters. Can. J. Fish. Aquat. Sci. 43: 108–123.

WYATT, T. 1972. Some effects of food density on the growth and behaviour of plaice larvae. Mar. Biol. 14: 210–216.

YIN, M. C., AND J. H. S. BLAXTER. 1987. Escape speeds of marine fish larvae during early development and starvation. Mar. Biol. 96: 459–468.

YOUNG, J. W., AND T. L. O. DAVIS. 1990. Feeding ecology of larvae of southern bluefin, albacore and skipjack tunas (Pisces: Scombridae) in the eastern Indian Ocean. Mar. Ecol. Prog. Ser. 61: 17–29.

Seasonal Habitat Selection and Preferences by Cutthroat Trout (*Oncorhynchus clarki*) in a Small, Coastal Stream

Jan Heggenes

Department of Biology and Nature Conservation, Agricultural University of Norway, Box 14, N-1432 Ås-NLH, Norway

Thomas G. Northcote

Department of Zoology, University of British Columbia, Vancouver, B.C. V6T 2A9, Canada

and Armin Peter

Swiss Federal Institute for Water Resources and Water Pollution, 6047 Kastanienbaum, Switzerland

Heggenes, J., T. G. Northcote, and A. Peter. 1991. Seasonal habitat selection and preferences by cutthroat trout (*Oncorhynchus clarki*) in a small, coastal stream. Can. J. Fish. Aquat. Sci. 48: 1364–1370.

Habitat selection by cutthroat trout (*Oncorhynchus clarki*) larger than 9 cm total length was monitored during winter and summer. The trout had strong preferences for depths >25 cm and areas where instream and overhead cover exceeded 40% of the local surface area. The fish selected a variety of substrate sizes. Stream areas with mean water velocities <20 cm/s were preferred. Compared with previous studies, the trout used low-velocity areas more, and we suggest that this is due to less competitive interaction from other young salmonids. The trout used the larger pools (>20 m^2) considerably less during winter than during summer. Otherwise, little seasonal variation in habitat use was found. A composite measure of water depth and cover appeared to be the most important of the measured environmental factors influencing habitat selection in the stream. The larger trout, which were presumably dominant, occupied the deepest pool areas. The trout selected spatial habitats in proportions significantly different from the available habitat, demonstrating strong habitat preferences. It is concluded that observations of habitat occupancy without considering habitat availability may give biased results.

On a surveillé au cours de l'hiver et de l'été la sélection de l'habitat par des truites fardées (*Oncorhynchus clarki*) dont la longueur totale dépassait 9 cm. Ces truites manifestaient de fortes préférences pour les profondeurs supérieures à 25 cm et les endroits où la couverture dans l'eau et aérienne dépassait 40 % de la superficie locale. Ces poissons choisissaient diverses tailles de substrat. Ils préféraient les zones ayant des vitesses d'écoulement moyennes inférieures à 20 cm/s. Par rapport aux études antérieures, la truite utilisait davantage les secteurs à faible vitesse, et nous croyons que ceci est dû à des interactions moins compétitives avec d'autres jeunes salmonidés. La truite utilisait beaucoup moins les grands bassins (supérieurs à 20 m^2) en hiver qu'en été; sinon, très peu de variations saisonnières de l'utilisation de l'habitat étaient observées. Une mesure composée de la profondeur de l'eau et de la couverture semblait être le plus important des facteurs environnementaux mesurés influençant la sélection de l'habitat dans le cours d'eau. Les plus grands poissons, qui étaient présumément dominants, occupaient les zones les plus profondes du bassin. Ils choisissaient des habitats spatiaux dans des proportions significativement différentes des habitats disponibles, ce qui démontre de fortes préférences en matière d'habitat. On a conclu que les observations des taux d'occupation de l'habitat qui ne tiennent pas compte de la disponibilité de l'habitat peuvent donner des résultats biaisés.

Received May 8, 1990
Accepted February 20, 1991
(JA566)

Reçu le 8 mai 1990
Accepté le 20 février 1991

Different species of salmonids living in small streams usually occupy only certain types of habitat, out of the wide range of habitats available in a stream. A wide variety of environmental factors may affect their spatial distribution and habitat selection, including physical factors such as water temperature, discharge, velocities, depth, substrate, and cover and biotic factors such as intra- and interspecies interactions. Knowledge about the spatial niche requirements of a particular species is a prerequisite for understanding its ecology. It is furthermore necessary in environmental impact studies and management schemes for mitigating negative effects of human activities and for enhancing fish production. Such knowledge, however, even when combined with habitat surveys, may not necessarily be a good predictor of population abundance (Platts and Nelson 1988) due to incomplete knowledge about physical and biological interactions (Scott and Shirvell 1987) and the confounding effects of other niche dimensions.

Habitat selection by a particular species of salmonid may be affected by the presence of other species (Fausch and White 1981; Gatz et al. 1987) and vary with age or size of the fish (Jenkins 1969; Karlstrøm 1977; Bachman 1984). Previous habitat studies of cutthroat trout (*Oncorhynchus clarki*) have focused on the young trout living sympatrically with other species in small streams (Moore and Gregory 1988; Bisson et al. 1988). Our purpose was to investigate habitat use by cutthroat trout of different sizes, and in a situation with less competitive interactions from other salmonid species, to see if habitat use was different. We studied a cutthroat trout population in Musqueam Creek, a small stream in coastal British Columbia (Northcote and Hartman 1988). The cutthroat trout were numerically dominant over other fish species during the study

period. Water temperature is known to affect behaviour by species of trout (Hartman 1963; Heggenes 1988a), but this has not been studied for cutthroat trout. A second objective was to examine seasonal habitat selection by cutthroat trout in the creek. Most studies of habitat requirements of salmonids in streams have focused on habitat use by fish, but without quantifying total available stream habitat. However, habitat availability may also influence habitat actually occupied by fish (DeGraaf and Bain 1986; Heggenes 1991). To help remove the influence of available habitat on habitat use, it has been suggested that habitat use should be corrected for habitat availability (Baldridge and Amos 1982; Parsons and Hubert 1988). Our third objective was therefore to establish habitat preferences for cutthroat trout in a stream and to assess the effect of habitat availability on trout occupancy of habitat. Our working hypothesis was that such an effect would be pronounced, particularly in a small stream where the availability of different habitat types may be limited.

Study Area

The Musqueam–Cutthroat Creek system (approximately 730 ha) was chosen for the study. It does not usually freeze over during winter, and cutthroat trout was the numerically dominant overwintering fish species (>80% of all observed fish), with juvenile coho salmon (*Oncorhynchus kisutch*) the only other numerically important species. Western brook lamprey (*Lampetra richardsoni*) and prickly sculpin (*Cottus asper*) were captured only on a few occasions. Musqueam Creek proper is a small stream typical of those inhabited by cutthroat trout over much of their Pacific coastal range, but not well studied. There are previous and ongoing studies in the stream (Northcote and Hartman 1988; Heggenes et al. 1991) that provide a detailed description of the stream. A highway culvert apparently has prevented anadromous fishes from gaining access to its upper reaches. This movement barrier represented the upper limit of the study area. Another road culvert 529 m downstream represented a large habitat change, as the creek downstream from this culvert is channelized and very slow flowing (<5 cm/s), so it was therefore chosen as the lower limit of the study area.

Methods

The study area was divided into 175 segments by making transects every 3 m along the stream. Transects were marked in the field with numbered sticks. All fish observations were made on these transects. Cutthroat trout were collected with a square wave pulsed DC backpack fish shocker (425 V, pulse width 6.5 ms, frequency 70 cps); the anode was a 15-cm diameter wand-mounted ring, and the effective radius was about 0.5–1 m. In order to diminish possible fright bias, we adopted the method of systematic point electrofishing (Moyle and Baltz 1985) to avoid pushing the anode forward in the water (Hearn and Kynard 1986). The electrode was placed at one to three points along each transect, depending on stream width. The distance between electrofishing points was kept approximately equal along and across the study stream. Total lengths of all captured fish were measured to the nearest millimetre. The position of fish >9 cm total length was noted at the point of first sighting rather than at the point of capture to reduce the effects of galvanotaxis (Gatz et al. 1987) and with distance in metres measured from the nearest transect and the stream bank. Thus, all observations could be referred to "cells" described by a set of habitat variables (Bovee 1982). The study period was from January 1 through August 31, 1988. The stream was sampled at 2-wk intervals and at approximately base flow (40 L/s) except in late July to early August when the waterflow was about 5 L/s. The period from January to mid-March is referred to as winter season, mid-March to mid-May as spring, and mid-May to August as summer. The water temperature was measured to the nearest 0.1°C on each sampling occasion. The transects were also used as reference for total available habitat description.

Physical characteristics of the habitat were measured in verticals every 20 cm across each transect at base flow. Stream width, and at each point total water depth, mean water column velocity (at 0.6 times total water depth), substratum particle size, and instream as well as overhead cover were measured. Widths and depths were measured to the nearest centimetre. Water velocities were measured with a Marsh-McBirney 201 EM water current meter fitted with a 3-cm-diameter measuring head. The dominant streambed material size was visually classified according to a modified Wentworth scale (Heggenes et al. 1991). The mean (index of coarseness) and standard deviation (index of heterogeneity) for each cell were computed from the recorded values according to Bain et al. (1985). Cover was estimated by viewing a rope from above. The rope was divided into 20-cm segments and was laid on the stream bottom perpendicular to the current along each transect. The percentage of the rope that was hidden from a view from directly above (in 10% increments from <10 to >90%) was estimated. Cover was defined as and classified into (1) submerged large organic debris, (2) other submerged structures beneath which fish can hide from view overhead, (3) stones or boulders, (4) undercut banks or (5) overhanging vegetation less than 50 cm above the water surface, (6) broken water surface, and (7) fine organic debris.

Values of habitat preference (D) were calculated from the formula of Jacobs (1974):

$$D = \frac{r - P}{(r + P) - 2rp}$$

where r = proportion of resource (i.e. habitat parameter measured) use by the fish and p = proportion of resource (i.e. habitat parameter measured) available in the environment. Thus, a D value of 0 would indicate that the habitat is used in proportion with its availability instream, i.e. no preferences. Values in the range from -0.1 to -1 indicate that the habitat is used less than would be expected from its availability, and correspondingly, values in the range from $+0.1$ to 1 indicate that it is used more than expected, i.e. habitat preferences. Habitat suitability curves for the habitat variables were developed using chi-square frequency analysis according to Bovee and Cochnauer (1977).

In most previously published studies on fish habitat selection, it has been assumed that observations for each fish represent one independent observation. Data in the present study have on occasion been collected from the same fish more than once during the course of the study (Heggenes et al. 1991), and the capture of one fish may have affected position of adjacent fishes. Considering the time interval between sampling (Schreck et al. 1976), we nevertheless assume that only a small error is induced by possible lack of independence (DeGraaf and Bain 1986). Habitat use by different fish of different sizes was examined by regressing the habitat variables measured on fish

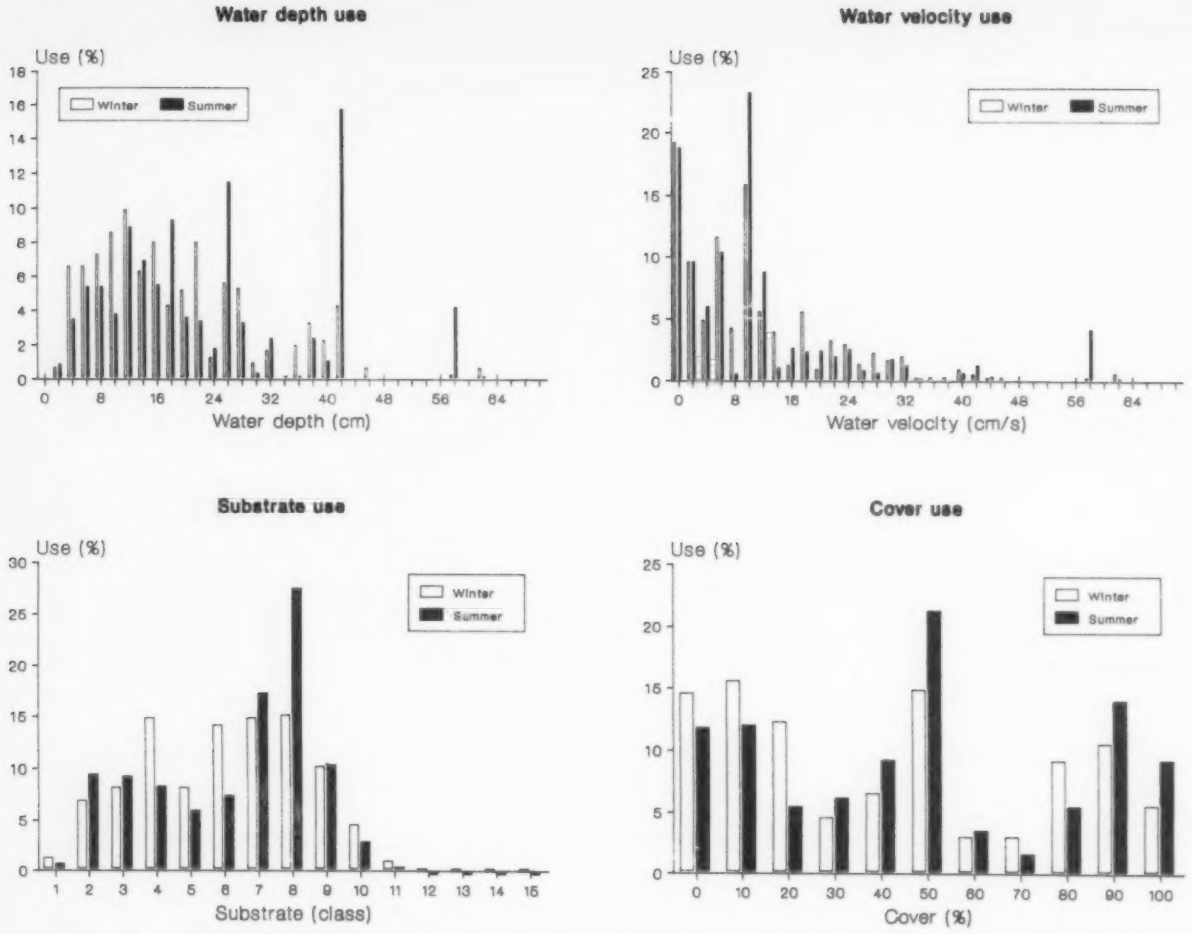


FIG. 1. Habitat use by Musqueam Creek cutthroat trout in winter (open bars) and summer (solid bars). Larger pools were in the depth ranges 25–30, 35–45, and 55–60 cm.

TABLE 1. Factor loadings and variance explained by principal components for habitat use by cutthroat trout in Musqueam Creek. Asterisks mark loadings considered to have contributed substantially to the principal components (loadings >0.61). Components with mineigen values >1 were retained.

Habitat variable	PC1 (42% of the variance)	PC2 (32% of the variance)
Water depth	85*	11
Cover	84*	7
Substrate	21	86*
Mean water velocity	−47	73*

length. Habitat use was compared between groups of fish by Kolmogorov–Smirnov tests for continuous variables and *G*-tests for discrete variables (Sokal and Rohlf 1981). Principal component analysis (SAS 1987) was used to identify components explaining observed variation in habitat use.

Results

Habitat Use

During the study, 754 observations of habitat use by cutthroat trout were made. Significant regressions between fish length and habitat use were found for water depth ($P = 0.0001$) and total amount of cover ($P = 0.008$). With increasing fish length, the cutthroat trout preferred deeper stream areas, but the proportion of variance of depth that was predictable was low ($R^2 = 0.04$). The R^2 between fish length and amount of cover was even weaker ($R^2 = 0.01$). Thus, within the trout length range studied (9–32 cm), length appeared to be of less importance in habitat selection. These low R^2 values were due, however, to the length distribution of the fish being skewed towards smaller fish (Heggenes et al. 1991). When habitat use was compared between the larger (>17 cm) and the smaller (<11 cm) trout, differences in water depth use were considerable (mean depth 26 cm, $n = 90$, compared with 18 cm, $n = 303$, $P < 0.01$, Kolmogorov–Smirnov test).

Variation in seasonal habitat use was identified (Fig. 1). During winter at water temperatures <6.3°C, the trout inhabited somewhat more shallow stream areas (mean depth 18 cm, $n = 302$) but moved towards deeper stream areas with increasing water temperatures in spring (8.1–10.0°C) (mean depth = 20 cm, $n = 108$) and occupied the deepest stream areas during summer at temperatures >10.9°C (mean depth = 22 cm, $n = 344$). In particular, a few large pools (Fig. 1;

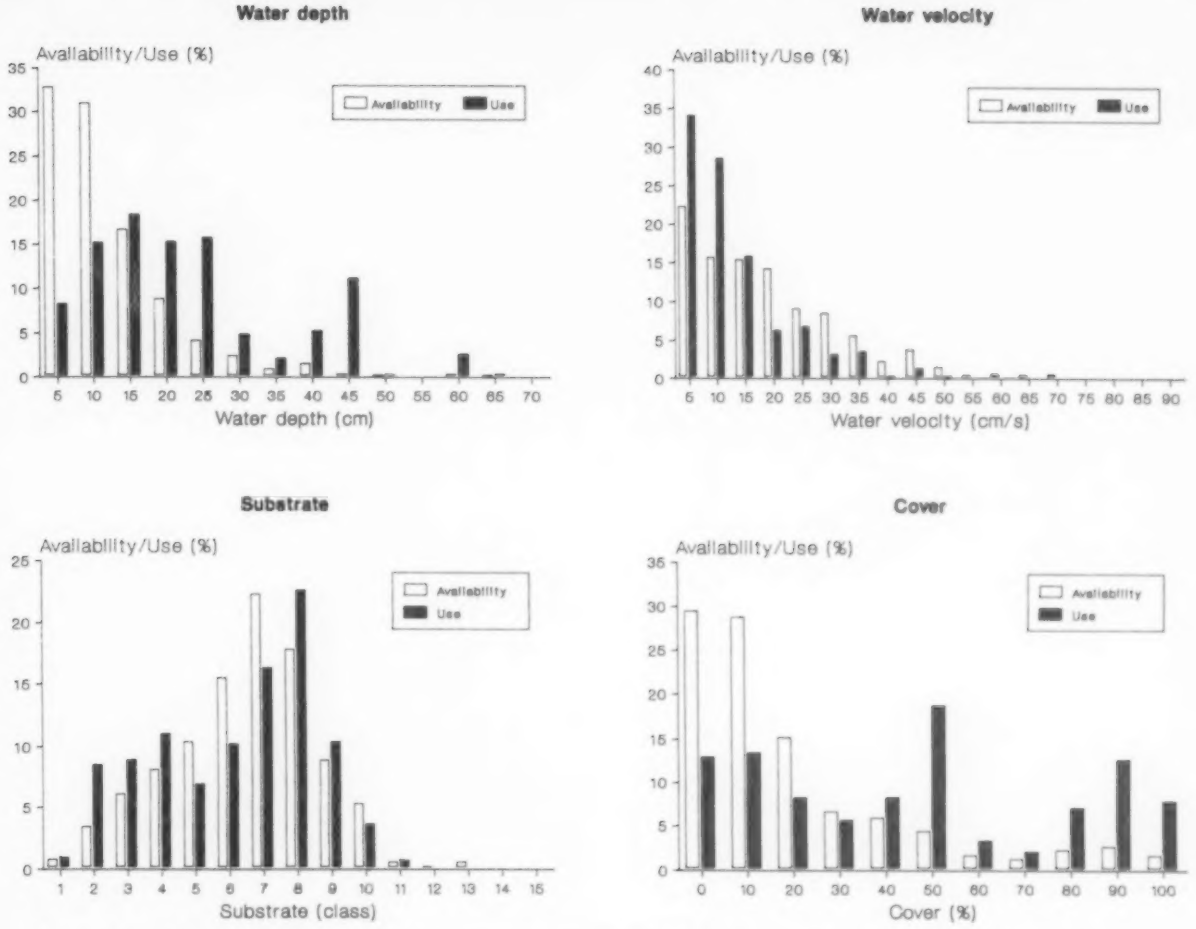


FIG. 2. Habitat availability (open bars) compared with pooled data for fish habitat use (solid bars) in Musqueam Creek.

depths 25–30, 40–45, and 55–60 cm) were used considerably more in summer than in winter.

Differences between winter and summer depth use were significant ($P < 0.01$, Kolomogorov–Smirnov test) and were not caused by any change in the length distribution of the fish present in the stream ($P = 0.60$, Kolmogorov–Smirnov test). The trout used slightly different substrate in summer than in winter (Fig. 1; $P < 0.01$, G-test). The trout selected habitats with significantly lower amounts of cover in winter than in summer (mean 42% compared with 48%, $P < 0.01$, G-test). There were no significant differences in cover type used ($P = 0.65$, G-test). The trout in cover used overhead cover more frequently (58.5%, $n = 402$; broken surface 31.8%, undercut banks 17.9%, overhanging vegetation 8.8%) than instream cover (41.5%; large organic debris 21.4%, fine organic debris 14.4%, stones and boulders 5.7%). At the extreme low flows in late July and early August, a comparison of mean values for water depth (mean depth = 23 cm at low flow, 22 cm during the rest of summer) and mean water velocity (mean velocity = 9 cm/s compared with 11 cm/s during the rest of summer) suggested a slightly stronger selection of pool areas at the extreme low summer flow in summer, but the differences were not significant ($P > 0.24$, Kolmogorov–Smirnov tests).

Multivariate Analysis

Examination of habitat use data by principal component analysis indicated that none of the variables alone explained much of the variance (Table 1). This result suggests that habitat selection is the result of a complex behaviour, perhaps also influenced by environmental factors other than the ones measured. Of the factors studied, a composite measure of water depth and cover appeared to be the most important one. Substrate was the dominant habitat variable in the second principal component, but mean water velocity was also of considerable importance. Thus, all the measured habitat variables appeared to influence habitat selection by cutthroat trout in this small stream.

Habitat Preferences

Use of the measured habitat variables by the trout was significantly different from measured availability of the habitat variables (Fig. 2), indicating clear preferences by the fish (Fig. 3). Compared with measured available habitat, the trout had strong preferences for the deeper stream areas both in winter and summer ($P < 0.01$, Kolmogorov–Smirnov test). Areas with higher (>20 cm/s) mean water velocities were used less intensively, and the trout preferred the more slow-flowing

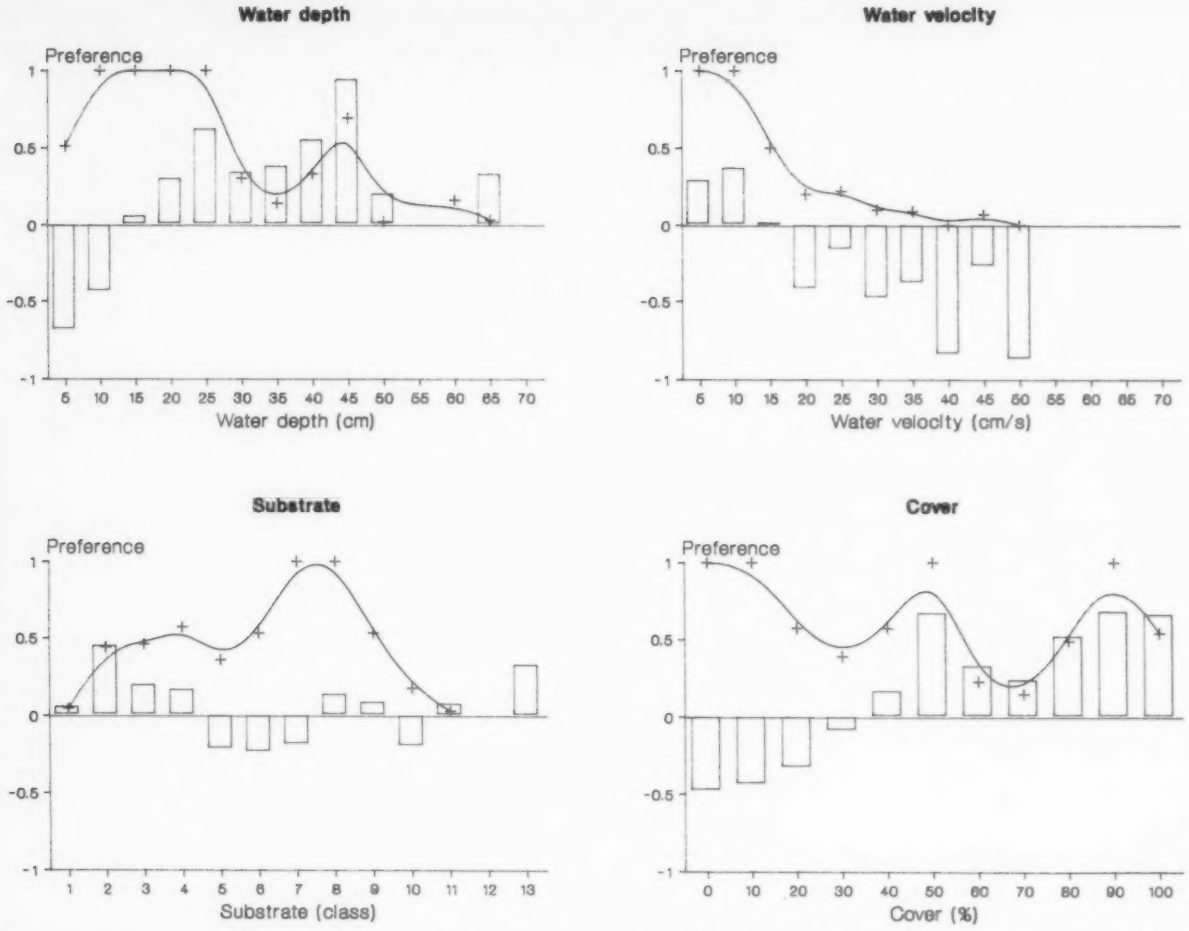


FIG. 3. Habitat preferences by Musqueam Creek cutthroat trout. Positive values indicate the habitat variable to be used more than expected from its availability in the stream, and negative values that it is used less than expected. Curves indicate habitat suitability based only on fish occupancy of habitat.

stream sections, provided they had suitable cover. The preferences for mean water velocities were not strong, except that the fish did not use the high-velocity areas. A high percentage of cover was preferred, and instream cover was preferred (28% of available cover, 41.5% of cover used), in particular organic debris (22.7% of available cover, 35.8% of cover used). Of the overhead cover types, undercut banks were preferred (10% of available cover, 17.9% of cover used). No particularly strong preferences for any of the available substratum particle sizes were found. The trout used a variety of particle sizes, provided that particularly water depth and cover were suitable.

Habitat suitability curves based on habitat use are also shown in Fig. 3. The suitability curves were different from the preference histograms, and in the case of amount of cover almost opposite. The habitat suitability curves apparently reflected habitat availability more than true trout habitat preferences.

Discussion

In the small stream we studied, the cutthroat trout used the deeper, slow-flowing stream areas with a high percentage of cover, while a variety of substrate sizes were used. Water depth and cover were apparently the more important environmental factors influencing habitat selection. The larger and presumably dominant (Jenkins 1969; Bachman 1984) cutthroat trout occupied the deeper pool areas. Studies of brown trout (*Salmo trutta*) have also indicated that larger fish are most abundant in deeper stream areas (Egglishaw and Shackley 1982; Kennedy and Strange 1986; Heggenes 1988b), but in contrast with our results, recent studies of rainbow (*Oncorhynchus mykiss*) and brown trout and Atlantic salmon (*Salmo salar*) in streams have ranked mean water velocity as the most important habitat variable (DeGraaf and Bain 1986; Gatz et al. 1987; Morantz et al. 1987; Heggenes and Saltveit 1989). Many factors may affect the ranking of habitat variables, such as habitat availability, waterflow and temperature regime, food supply, population density, and species interactions. Also, different habitat factors may be limiting in different streams (Fausch and White 1981; Heggenes 1988b; Parsons and Hubert 1988). Above all, it appears that depth, cover, substrate, and velocity interact strongly in habitat selection by cutthroat trout. We suggest that water depth was a very important habitat factor, particularly for the larger trout

in Musqueam Creek, probably because it is such a small stream. Deeper stream areas (>25 cm deep) were in short supply (less than 8.3% of the available habitat areas). The cutthroat trout utilized deep and slow-flowing habitats more often than has previously been reported for trout in sympatry with coho salmon and steelhead (Bisson et al. 1988), where it selected swiftly flowing habitats intermediate between coho and steelhead. Because of limits on availability of preferred habitat and competitive interactions, the observed habitat use by salmonids in different streams may not reflect choice, and competition can restrict the fish to less preferred habitat areas (Shirvell and Dungey 1983). Compared with the results reported by Bisson et al. (1988), our data suggest that cutthroat trout use more slow-flowing habitats in streams where numerically dominant and thus are prone to habitat displacement in streams where coho salmon are more abundant.

Differences in seasonal habitat selection by cutthroat trout were demonstrated in the present study. The main difference in winter habitat selection was, unexpectedly, that some trout abandoned the larger pools. Young salmonids appear to have stronger preferences for cover and particularly seek shelter in the substrate at low temperatures (Chapman and Bjornn 1969; Bustard and Narver 1975a, 1975b; Rimmer et al. 1983, 1984; Heggenes and Saltveit 1989). Cunjak (1988) also found that young Atlantic salmon did not use pool areas extensively during low water temperatures in winter. However, these studies have focused on young (i.e. smaller) fish, and there has been less knowledge as to the winter habitat selection by larger fish. A substantial proportion of the cutthroat trout population in Musqueam Creek was made up of smaller fish, and therefore we had expected to observe more use of coarse substrate providing interstices to hide in during winter than during summer. Bjornn (1971) observed rainbow trout to emigrate downstream to overwinter in coarse rubble of the Lehmi River. However, no such change in substrate use was found in Musqueam Creek. But the availablity of coarser substrate was restricted, which may be part of the explanation. Because of the restricted availability of coarse substrate, we had expected larger fish to remain in or move to the deep, sheltered pool areas during winter, and therefore more use of this type of habitat. Surprisingly, we observed less use of such habitats in winter. Some of the shallower winter habitat areas provided undercut banks in shallower water, which may have attracted fish in winter. Cooper (1953) noted that brook trout (*Salvelinus fontinalis*) moved from pools into dense cover in winter.

Our results demonstrated that habitat selection data based on fish occupancy of habitat may be a poor indicator of what is suitable habitat for a fish species. Fish may occupy stream areas because they choose to or because they have to. In Musqueam Creek, habitat suitability curves based on trout habitat use reflected habitat availability more than they reflected habitat suitability. The preference values, where habitat use was corrected for habitat availability, indicated optimal cutthroat habitat to be clearly different from what the habitat use data suggested. Habitat suitability curves based on fish habitat use are of little value, unless the entire range of all the habitat variables are equally well represented within the stream(s) studied (Morantz et al. 1987). However, as all streams are different, this will rarely be the case. Thus, quantification of total available aquatic habitat ought to be included in all fish habitat selection studies, so that habitat use can be considered in relation to habitat availability.

Acknowledgements

The authors give special thanks to D. Atagi for help in the field work. This work was financed in large part by the Norwegian Agricultural Sciences Research Council and in small part by NAVF Fiskeforsterkningstiltak and the Natural Sciences and Engineering Research Council of Canada.

References

BACHMAN, R. A. 1984. Foraging behavior of free-ranging wild and hatchery brown trout in a stream. Trans. Am. Fish. Soc. 113: 1–32.

BAIN, M. B., J. F. FINN, AND H. E. BOOKE. 1985. Quantifying stream substrate for habitat analysis studies. N. Am. J. Fish. Manage. 5: 499–506.

BALDRIDGE, J. E., AND D. AMOS. 1982. A technique for determining fish habitat suitability criteria: a comparison between habitat utilization and availability, p. 251–258. *In* N. B. Armantrout [ed.] Acquisition and utilization of aquatic habitat inventory information. American Fisheries Society, Western Division, Bethesda, MD.

BISSON, P. A., K. SULLIVAN, AND J. L. NIELSEN. 1988. Channel hydraulics, habitat use and body form of juvenile coho salmon, steelhead, and cutthroat trout in streams. Trans. Am. Fish. Soc. 117: 262–273.

BJORNN, T. C. 1971. Trout and salmon movements in two Idaho streams as related to temperature, food, stream flow, cover and population density. Trans. Am. Fish. Soc. 100: 423–438.

BOVEE, K. 1982. A guide to stream habitat analysis using the Instream Flow Incremental Methodology. Instream Flow Inf. Pap. 12. U.S. Fish Wildl. Serv. FWS/OBS-82/26: 248 p.

BOVEE, K., AND T. COCHNAUER. 1977. Development and evaluation of weighted criteria, probability of use curves for instream flow assessment: fisheries. Instream Flow Inf. Pap. 3. U.S. Fish Wildl. Serv. FWS/OBS-77/63: 38 p.

BUSTARD, D. R., AND D. W. NARVER. 1975a. Aspects of the winter ecology of juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*Salmo gairdneri*). J. Fish. Res. Board Can. 32: 667–680.

1975b. Preferences of juvenile coho salmon (*Oncorhynchus kisutch*) and cutthroat trout (*Salmo clarki*) relative to simulated alteration of winter habitat. J. Fish. Res. Board Can. 32: 681–687.

CHAPMAN, D. W., AND T. C. BJORNN. 1969. Distribution of salmonids in streams, with special reference to food and feeding, p. 153–176. *In* T. G. Northcote [ed.] Symposium on salmon and trout in streams. University of British Columbia, Vancouver, B.C.

COOPER, E. L. 1953. Periodicity of growth and change of condition of brook trout (*Salvelinus fontinalis*) in three Michigan trout streams. Copeia 1953: 107–114.

CUNJAK, R. A. 1988. Behaviour and microhabitat of young Atlantic salmon (*Salmo salar*) during winter. Can. J. Fish. Aquat. Sci. 45: 2156–2160.

DEGRAAF, D. A., AND L. H. BAIN. 1986. Habitat use by and preferences of juvenile Atlantic salmon in two Newfoundland rivers. Trans. Am. Fish. Soc. 115: 671–681.

EGGLISHAW, J. H., AND P. E. SHACKLEY. 1982. Influence of water depth on dispersion of juvenile salmonids, *Salmo salar* L. and *S. trutta* L., in a Scottish stream. J. Fish Biol. 21: 141–156.

FAUSCH, K. D., AND R. S. WHITE. 1981. Competition between brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*) in a Michigan stream. Can. J. Fish. Aquat. Sci. 38: 1220–1227.

GATZ, A. J. JR., M. J. SALE, AND J. M. LOAR. 1987. Habitat shifts in rainbow trout: competitive influences of brown trout. Oecologia (Berl.) 74: 7–19.

HARTMAN, G. F. 1963. Observations on the behaviour of juvenile brown trout in a stream aquarium during winter and spring. J. Fish. Res. Board Can. 20: 769–787.

HEARN, W. E., AND B. E. KYNARD. 1986. Habitat utilization and behavioral interaction of juvenile Atlantic salmon (*Salmo salar*) and rainbow trout (*S. gairdneri*) in tributaries of the White River of Vermont. Can. J. Fish. Aquat. Sci. 43: 1988–1998.

HEGGENES, J. 1988a. Substrate preferences by brown trout fry (*Salmo trutta*) in artificial stream channels. Can. J. Fish. Aquat. Sci. 45: 1801–1806.

1988b. Effect of experimentally increased intraspecific competition on sedentary adult brown trout (*Salmo trutta*) movement and stream habitat choice. Can. J. Fish. Aquat. Sci. 45: 1163–1172.

1991. Comparison of habitat selection and preferences by an allopatric cohort of juvenile Atlantic salmon (*Salmo salar*) under conditions of low competition in a Norwegian stream. Holarc. Ecol. 14: 51–62.

HEGGENES, J., T. G. NORTHCOTE, AND A. PETER. 1991. Spatial stability of cutthroat trout (*Oncorhynchus clarki*) in a small, coastal stream. Can. J. Fish. Aquat. Sci. 48: 757–762.

HEGGENES, J., AND S. J. SALTVEIT. 1989. Seasonal and spatial microhabitat selection and segregation in young Atlantic salmon, *Salmo salar* L., and brown trout, *S. trutta* L., in a Norwegian river. J. Fish Biol. 36: 707–720.

JACOBS, J. 1974. Quantitative measurement of food selection: a modification of the forage ratio and Ivlevs electivity index. Oecologia 14: 413–417.

JENKINS, T. M. JR. 1969. Social structure, position choice and micro distribution of two trout species (*S. trutta* and *gairdneri*) resident in mountain streams. Anim. Behav. Monogr. 2: 57–124.

KARLSTRØM, Ø. 1977. Habitat selection and population densities of salmon (*Salmo salar* L.) and trout (*S. trutta* L.) parr in Swedish rivers with some reference to human activities. Acta Univ. Ups. 404: 12 p.

KENNEDY, G. J. A., AND C. D. STRANGE. 1986. The effects of intra- and interspecific competition on the distribution of stocked juvenile Atlantic salmon, *Salmo salar* L., in relation to depth and gradient in an upland trout, *Salmo trutta* L., stream. J. Fish Biol. 29: 199–214.

MOORE, K. M. S., AND S. V. GREGORY. 1988. Response of young-of-the-year cutthroat trout to manipulation of habitat structure in a small stream. Trans. Am. Fish. Soc. 117: 162–170.

MORANTZ, D. L., R. K. SWEENEY, C. S. SHIRVELL, AND D. A. LONGARD. 1987. Selection of microhabitat in summer by juvenile Atlantic salmon (*Salmo salar*). Can. J. Fish. Aquat. Sci. 44: 120–129.

MOYLE, P. B., AND D. M. BALTZ. 1985. Microhabitat use by an assemblage of California stream fishes: developing criteria for instream flow determinations. Trans. Am. Fish. Soc. 114: 695–704.

NORTHCOTE, T. G., AND G. F. HARTMAN. 1988. The biology and significance of stream trout populations (*Salmo* spp.) living above and below waterfalls. Pol. Arch. Hydrobiol. 35: 409–442.

PARSONS, G. M., AND W. A. HUBERT. 1988. Influence of habitat availability on spawning site selection of Kokanees in streams. N. Am. J. Fish. Manage. 8: 426–431.

PLATTS, W. S., AND R. L. NELSON. 1988. Fluctuations in trout populations and their implications for land-use evaluation. N. Am. J. Fish. Manage. 8: 333–345.

RIMMER, D. M., U. PAIM, AND R. L. SAUNDERS. 1983. Autumnal habitat shift of juvenile Atlantic salmon (*Salmo salar*) in a small river. Can. J. Fish. Aquat. Sci. 40: 671–680.

1984. Changes in the selection of microhabitat by juvenile Atlantic salmon (*Salmo salar*) at the summer–autumn transition in a small river. Can. J. Fish. Aquat. Sci. 41: 469–475.

SAS. 1987. SAS/STAT guide for personal computers: the PRINCOMP procedure. SAS Institute Inc., Cary, NC. 1029 p.

SCHRECK, C. B., R. A. WHALEY, M. L. BASS, O. E. MAUGHAN, AND M. SOLAZZI. 1976. Physiologic responses of rainbow trout (*Salmo gairdneri*) to electroshock. J. Fish. Res. Board Can. 33: 76–84.

SCOTT, D., AND C. S. SHIRVELL. 1987. A critique of the instream flow incremental methodology with observations on flow determination in New Zealand, p. 27–43. *In* B. Kemper and J. F. Craig [ed.] Regulated streams: advances in ecology. Plenum Press, New York, NY.

SHIRVELL, C. S., AND R. G. DUNGEY. 1983. Microhabitats chosen by brown trout for feeding and spawning in rivers. Trans. Am. Fish. Soc. 112: 355–367.

SOKAL, R. R., AND F. J. ROHLF. 1981. Biometry. Freeman, New York, NY. 859 p.

Impact of Bleached Kraft Mill Effluent on Population Characteristics, Liver MFO Activity, and Serum Steroid Levels of a Lake Superior White Sucker (*Catostomus commersoni*) Population

K. R. Munkittrick[1]

Department of Zoology, University of Guelph, Guelph, Ont. N1G 2W1, Canada

C. B. Portt

C. Portt and Associates, 56 Waterloo Avenue, Guelph, Ont. N1H 3H5, Canada

G. J. Van Der Kraak

Department of Zoology, University of Guelph, Guelph, Ont. N1G 2W1, Canada

and I. R. Smith and D. A. Rokosh

Biohazards Unit, Aquatic Biology Section, Water Resources Branch, Ontario Ministry of the Environment, Rexdale, Ont. M9W 5L1, Canada

Munkittrick, K. R., C. B. Portt, G. J. Van Der Kraak, I. R. Smith, and D. A. Rokosh. 1991. Impact of bleached kraft mill effluent on population characteristics, liver MFO activity, and serum steroid levels of a Lake Superior white sucker (*Catostomus commersoni*) population. Can. J. Fish. Aquat. Sci. 48: 1371–1380.

White sucker (*Catostomus commersoni*) collected from a site receiving primary-treated bleached kraft mill effluent (BKME) were older and had a higher condition factor than fish at a reference site and grew more slowly than fish from three other areas of Lake Superior. The BKME-exposed fish also exhibited an increased age to maturity, smaller gonads, lower fecundity with age, an absence of secondary sex characteristics in males, and females failed to show an increase in egg size with age. Lower serum estradiol and testosterone concentrations and greater hepatic mixed-function oxidase (MFO) activity, as measured by conversion of diphenyloxazole and benzo[a]pyrene were also observed in the BKME-exposed fish. The level of MFO activity varied with season; differences could not be detected between sites during the spring spawning period, but were markedly elevated (up to ninefold) at the BKME site during the summer. The poorer performance of fish at the BKME site appears to be related to decreased levels of serum steroids and consequent abnormalities in reproductive development and carbohydrate metabolism, although the relationship of the changes in steroid levels with the increased hepatic enzyme activity remains to be established.

Les meuniers noirs (*Catostomus commersoni*) d'un site recevant les effluents d'une usine de pâte kraft blanchie déversés après un traitement primaire (EUPKB) étaient plus vieux et caractérisés par un facteur de condition supérieur à celui des poisson d'un site de référence, et ils croissaient plus lentement que les poissons de trois autres secteurs du lac Supérieur. Les poissons exposés aux EUPKB étaient également caractérisés par un âge supérieur à maturité, de plus petites gonades, une plus faible fécondité vaec l'âge, et l'absence de caractéristiques sexuelles secondaires chez les mâles, et de plus, les oeufs des femelles ne présentaient pas d'augmentation de taille avec l'âge. On a également observé de plus faibles concentrations d'estradiol et de testostérone dans le sérum et une plus forte activité des enzymes hépatiques MFO, selon des mesures de conversion du diphényl-oxazole et du benzo[a]pyrène dans le poisson exposé aux EUPKB. Le niveau d'activité des enzymes MFO variait selon les saisons et on ne pouvait déceler de différences d'un site à l'autre au cours de la période du frai printanier, mais elles étaient beaucoup plus fortes (jusqu'à neuf fois plus élevées) à l'emplacement à EUPKB au cours de l'été. Le plus faible rendement des poissons du site recevant des EUPKB semble être en rapport avec les plus faibles teneurs en stéroïdes du sérum et d'anomalies qui s'ensuivent, touchant le développement de l'appareil reproducteur et du métabolisme des glucides, bien que le rapport entre les changements des teneurs en stéroïdes et l'activité enzymatique hépatique restent à établir.

Received June 25, 1990
Accepted February 20, 1991
(JA624)

Reçu le 25 juin 1990
Accepté le 20 février 1991

There is a lack of understanding of the influence of both untreated and treated effluents from the pulp and paper industry on the early developmental life stages of sensitive aquatic organisms and their reproduction and resistance to disease (McLeay 1987). Until recently, studies of fish in the field have usually been restricted to captive fish (reviewed in McLeay 1987), and very few receiving-water studies have attempted to define the zone of influence affected by an isolated "point-source" bleached kraft mill effluent (BKME). Although many changes have been documented at specific sites, the interpretation of results has often been complicated by other confounding factors, such as additional effluent sources. As a con-

[1]Present address: Department of Fisheries and Oceans, Great Lakes Laboratory for Fisheries and Aquatic Sciences, 867 Lakeshore Road, P.O. Box 5050, Burlington, Ont. L7R 4A6, Canada.

sequence, few studies were capable of linking these changes either directly or indirectly to pulp and paper effluents or to fisheries resources.

Over the past few years, Swedish field studies have documented low-level BKME impacts on fish community structure, growth, carbohydrate metabolism, maturation, recruitment, and mortality (Andersson et al. 1987, 1988; Larsson et al. 1988; Neuman and Karås 1988; Sandström and Thoresson 1988; Sandström et al. 1988; Böhling et al. 1991; Karås et al. 1991), and some changes were evident at distances greater than 8 km from a BKME outfall receiving only primary treatment (Andersson et al. 1988). Sandström et al. (1988) described a decrease in the percentage of mature fish developing gonads, a decrease in gonadal weight, and an increase in condition factor associated with primary-treated BKME. Andersson et al. (1988) reported decreased gonad growth, increased liver size, a 10-fold increase in liver mixed-function oxidase (MFO) activity, abnormal carbohydrate metabolism, changes in haematology, and increased fin erosion. Although the Swedish investigations of physiological and biochemical impacts were extensive, the studies did not provide evidence of a mechanism to explain the changes.

The Scandinavian studies have been criticized in part because of the paucity of supporting studies from North American pulp mills. The absence of supporting data has been attributed to a number of differences, including confounding industrial discharges and habitat conditions in the Baltic region (Sprague and Colodey 1989). Although the Swedish studies showed evidence of impact of dilution levels of 1:1000 to 1:2000, there are North American situations where pulp mill effluent present at concentrations above 1% has not been associated with adverse impacts (reviewed in Sprague and Colodey 1989). Sprague and Colodey (1989) postulated that these differences could be explained by the concomitant action of other toxicants in the Baltic Sea but cautioned that the absence of substantial published details prevented independent validation of BKME impacts.

This study was designed to examine the population characteristics, biochemical changes, and reproductive development of a white sucker (*Catostomus commersoni*) population collected from Jackfish Bay, Lake Superior, for evidence of BKME-associated impacts. Effluent from the Kimberley-Clark pulp mill at Terrace Bay, Ontario, received only primary treatment (until September of 1989) prior to dilution in Jackfish Bay. Jackfish Bay is relatively isolated and provided an ideal situation to test for the impact of primary-treated BKME on wild fish populations. White sucker are abundant in the region and have been shown to be a good indicator of contaminant impact (Munkittrick and Dixon 1989a; Smith et al. 1991).

Methods

Study Site

The bleached kraft mill at Terrace Bay produces approximately 1200 air-dried metric tons of pulp per day and discharges approximately 121 200 m^3 of effluent per day (>70 000 $L \cdot min^{-1}$) into Blackbird Creek. Blackbird Creek flows 15 km away from town to Jackfish Bay, which is relatively isolated and receives no industrial or municipal effluents other than the BKME. Although an aerated lagoon was installed as secondary treatment, it did not become operational until late September 1989. At the time of our study (May–August 1988), the only treatment that effluent received was passage of the main mill effluent through two clarifiers. Chemical characterization of the effluent was not available, but Flood et al. (1986) reported elevated levels of waterborne resin acids (total >2 $mg \cdot L^{-1}$) in Jackfish Bay and elevated levels of chlorophenols in rainbow trout (*Oncorhynchus mykiss*) caged in Jackfish Bay. Caged fish bioassays conducted in 1983 found 100% mortality 1.5 km off the mouth of Blackbird Creek. Based on 1984–86 bioassay data conducted at the mouth of Blackbird Creek, 96-h LC50 values ranged from <10 to 45.6% (International Joint Commission (IJC) 1989). These data are not directly comparable with the situation which existed at the time of the 1988 survey, due to changes to in-plant operations. However, primary-treated effluent was discharged into the bay from 1949 until 1989. At the time of the 1988 survey, definite water temperature, colour, and turbidity problems existed up to several kilometres off the creek mouth, and wood fibres were evident in fish stomachs. Sediment core profiles of dioxins and furans contained elevated TCDF (>2 $ng \cdot g^{-1}$) dating back to 1973, and levels of total TCDD in white sucker collected in 1989 were 7 $pg \cdot g^{-1}$ and of TCDF were 44 $pg \cdot g^{-1}$ ($n = 4$; 1.73% lipid) (Sherman et al. 1990). Studies conducted prior to the initiation of secondary treatment have concluded that "a 5 km^2 area of Moberley Bay and Jackfish Bay has been altered to an extent that normal clean-water bottom-dwelling organisms are not able to survive and have been replaced by pollution-tolerant forms. This is a result of direct toxic influences of the effluent or deposition of organic wastes" (IJC 1989).

Collections

Spawning fish were collected from Sawmill Creek, which is not exposed to BKME. The spawning fish leave Jackfish Bay and travel through Tunnel Bay to Jackfish Lake and into Sawmill Creek for spawning (Fig. 1). Jackfish Lake was part of Lake Superior prior to construction of the Canadian National Railway early in the century. There are a few residents on Jackfish Lake, but no permanent residents on Jackfish Bay and no industrial development on either site. Except for two streams entering Jackfish Lake, there are no suitable spawning streams for white sucker within the Jackfish Bay drainage. The duration of residency in clean water prior to spawning is unknown, but impacts on serum steroid hormone levels, associated with effluent exposure, are still evident in fish collected from the spawning beds (G. J. Van Der Kraak, M. E. McMaster, and K. R. Munkittrick, unpubl. data).

During the summer collections, the fish were collected approximately 500 m off the mouth of Blackbird Creek. Jackfish Bay is a relatively shallow bay; the fish were collected in approximately 10 m of water. The surrounding area of Lake Superior drops to more than 60 m water depth, and white sucker are not typically captured in depths >15 m in Lake Superior. It would appear that white sucker captured in this area during the summer are resident fish. Approximately 100 white sucker of each sex were collected from the upstream spawning migrations in Sawmill Creek (draining into Jackfish Bay) and the Little Gravel River (draining into the reference site at Mountain Bay) (Fig. 1) by overnight hoop net sets in May 1988. During August 1988, white sucker were collected from under the effluent plume in Jackfish Bay and from Mountain Bay using 10-cm stretch mesh gill net, set in 4–10 m of water. Fork length (millimetres) and total wet weight were determined for each

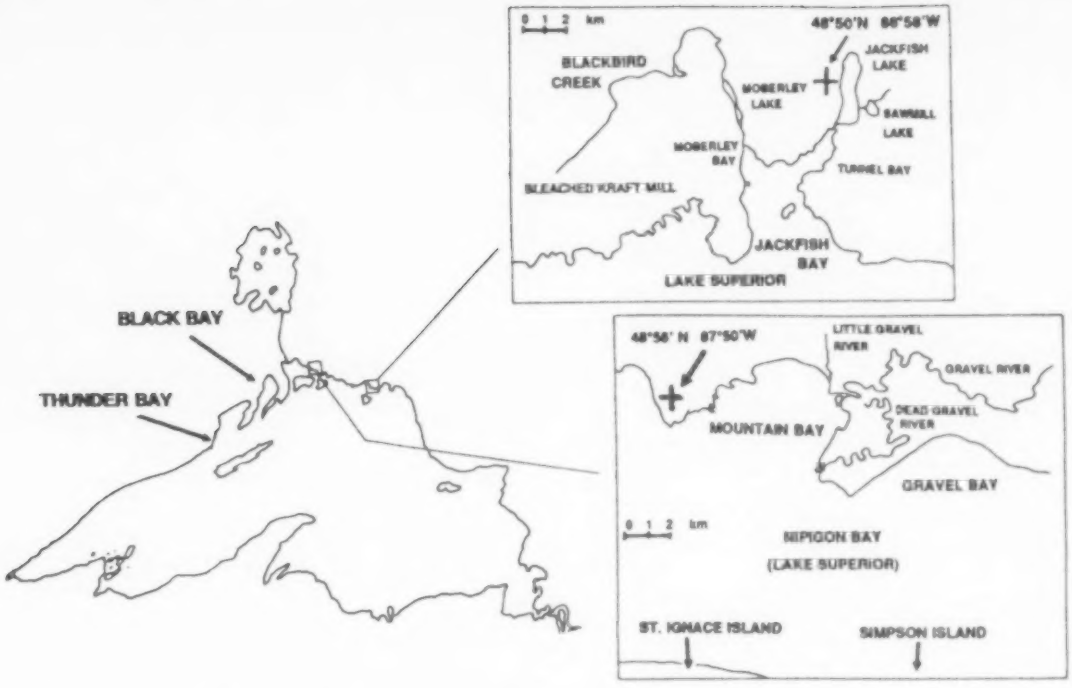


FIG. 1. Study site. Effluent from the bleached kraft mill at Terrace Bay, Ontario, reaches Lake Superior at Jackfish Bay.

fish, an opercular bone was removed for subsequent aging, and each fish was examined for both external and internal lesions.

In the spring, ovaries were removed, weighed (±0.1 g), and 1-g samples of ovarian tissue from prespawning fish were preserved in 10% formalin. All gonad weights were conducted on prespawning fish only. Fish which had ovulated eggs in the body cavity were not used in the analysis. Samples were returned to the laboratory, where the mean diameter of samples of 10 eggs (±0.1 mm) and the number of eggs in duplicate subsamples (0.1–0.2 g) of ovarian tissue were determined. From these data, fecundity (total number of eggs per female), gonadosomatic index (GSI = 100 × gonad wt/(total − gonad wt)) and condition factor (k = 100 × wt/length^3) were estimated.

Blood samples were collected in August by caudal severance, allowed to clot on ice, and the serum was frozen in liquid nitrogen for transport back to the laboratory. Testosterone and 17β-estradiol were measured by radioimmunoassay (RIA) in serum following ether extraction. A description of the antisera used to measure testosterone was reported in Van Der Kraak et al. (1984) and for estradiol in Van Der Kraak et al. (1990). Measurement of estradiol and testosterone followed the description of Van Der Kraak et al. (1984). All plasma samples were assayed in duplicate and interassay variability was less than 15% in both RIA systems. Total serum L-thyroxine (T4) and triiodo-L-thyronine (T3) concentrations were assayed using a double-antibody RIA (Jolden Diagnostics, Scarborough, Ont.) which has been described previously (Burke and Leatherland 1983).

Mixed Function Oxidase Determination

Liver tissue was minced in cold 1.0% KCl, frozen in capped vials in liquid nitrogen, and stored at −80°C until analysis. In the laboratory, the samples were thawed on ice and analyzed for MFO activity using 2,5-diphenyloxazole (PPO) and benzo[*a*]pyrene (BaP) as substrates. The PPO assay (for aryl hydrocarbon hydroxylase activity; AHH) has been used most recently as a substitute for the BaP assay of AHH activity. It has several advantages, including the lower carcinogenicity of the parent compound. There were no differences in PPO measurements conducted on postmitochondrial supernatant (PMS), relative to measurements using the 100 000 × g microsomal preparation (unpublished data). Similar evidence was not available for BaP assays, so microsomal preparations were used. Protein content was determined by the Bradford binding assay (Bradford 1976), using bovine serum albumin as the standard.

For MFO activity against PPO, the samples were homogenized with two volumes (v/w) of homogenizing buffer containing 50 mM Tris (pH 7.5) with 3.0 mM $MgCl_2$ and 0.2 M KCl (after Luxon et al. 1987). After centrifugation at 9000 × g (PMS) for 20 min, the supernatant was used fresh in subsequent analysis (after Luxon et al. 1987) as follows: 250 μL of Tris buffer was added to 500 μL of distilled water, 100 μL of 3.7 mM reduced nicotinamide adenine dinucleotide phosphate (NADPH), 100 μL of supernatant, and 50 μL of 9.04 M PPO. Controls (reagent blanks) were performed as above, except that 1.0 mL of acetone was added prior to the PPO. Duplicate tubes were analyzed at each time (10 and 20 min), adding 1.0 mL of acetone to stop the reaction. Tubes were extracted with 3.25 mL of hexane, and 2.0 mL of the organic phase was extracted with 5.0 mL of 1.0 M NaOH. The fluorescence of the NaOH fraction was analyzed in a Turner model 112 fluorometer with a No. 8 emission filter following a No. 7-60 excitation filter. Measured fluorescence arose from activation at 320–390 nm, with emission at >485 nm.

For MFO activity against BaP, the liver samples were homogenized with a motorized teflon mortar and pestle with two volumes (v/w) of homogenizing buffer, 0.1 M HPO_4 buffer (pH 7.4), 1 mM dithiothreitol, 1 mM EDTA, and 20% glycerol. Supernatant after 9000 × *g* centrifugation (PMS) was centrifuged at 100 000 × *g* for 1 h to sediment the microsomes. Microsomes were resuspended in 1 mL buffer·g wet wt^{-1}, yielding 15–25 mg protein·mL^{-1}. Activity was determined by a modification of Nebert and Gelboin (1968): 0.85 mL buffer (50 mM Tris–HCl, 3 mM $MgCl_2$) plus 0.1 mL of enzyme preparation (approximately 1 mg of liver protein per tube after dilution with homogenizing buffer), 0.01 mL NADPH (7.2 mM), and 0.04 mL (80 mM) of BaP were combined in a 16 × 100 mm screw-top tube and duplicates were incubated with shaking at 27°C for 30 min. Blanks were made by adding acetone before the BaP. The reaction was stopped with the addition of acetone, followed by extraction with 3.25 mL of hexane. Two millilitres of the hexane layer was back-extracted with 5 mL of 1.0 M NaOH, and the fluorescence was read in the NaOH layer. Fluorescence was determined in a Turner model 112 fluorometer with a No. 7-60 excitation filter and No. 2A-12 emission filter, measured fluorescence (>510 nm) resulting from excitation between 320 and 390 nm.

Mean MFO activity of the replicates at each time was corrected for the blanks and converted to arbitrary fluorescence units per milligram of protein per minute, and the specific activities of these two times were averaged for PPO.

Statistics

Site differences in length, weight, fecundity, and condition factor were compared using one-way ANOVA of log-transformed values. Age and steroid comparisons were carried out using Mann–Whitney *U*-tests. The relationships between fork length and age, body weight, gonad weight, and egg weight were examined using ANCOVA of log-transformed values, with location of capture as the covariate.

Results

Male and female white sucker collected from Jackfish Bay (BKME site) were significantly shorter than those from Mountain Bay (reference site) during both seasons (Table 1) and with the exception of spawning males ($p = 0.058$) were also significantly lighter. The BKME fish also showed increased condition factor during both seasons ($p < 0.001$). There were no differences in the slopes of regressions of fork length versus body weight (total weight minus gonad weight) for either males or females (ANCOVA, log-transformed data; $p = 0.43$ and 0.66, respectively), but intercepts differed significantly between sites ($p < 0.001$, $r^2 = 0.94$ and 0.89, respectively). During the summer, there was a marginal difference in the slopes of weight versus length for male fish ($p = 0.046$), but no difference for females ($p = 0.60$). Intercepts were significantly different between sites for both sexes ($p < 0.001$; $r^2 = 0.73$ and 0.84, respectively). The lower r^2 during the summer samples was related to the decrease in the size range of fish in samples collected by gill net (summer) relative to the spawning run (Fig. 2). The BKME spawning male sucker ranged in weight from 288 to 1323 g, while the gillnet samples ranged from 706 to 1170 g. The age distribution of females during the August sample was shifted towards older fish, coincident with the decreased growth rate and the size-selective nature of the gillnet captures.

Both male and female fish were older at the BKME site during the spawning run ($p < 0.001$) (Fig. 3). During the summer sampling period, females were significantly older at the BKME site ($p = 0.025$) but males were not ($p = 0.063$). Logarithmic age regressions of spawning fish were different between sites for both males and females (ANCOVA, $p < 0.001$; $r^2 = 0.60$ for males and 0.63 for females). Sucker collected during the summer showed no significant differences between Jackfish Bay and Mountain Bay, due to biases associated with the size-selective net gear, although the trends were consistent with those seen during the spawning period (Fig. 4). Fish from the spawning run were collected with hoop nets which were set across the spawning streams to collect all fish ascending the streams. The mean age of youngest 30 male fish and the youngest 30 female fish (of 100 sampled) from the reference site was significantly less than at the BKME site (Table 2). There were no differences between sites in either length ($p = 0.59$) or weight ($p = 0.56$) of male fish at the age of maturity, although females at the BKME site were shorter ($p<0.001$), lighter ($p =$

TABLE 1. Length, age, weight, condition, factor, GSI, and fecundity of white sucker exposed to BKME. Values are reported as mean ± SEM (*n*). Statistical difference from reference site: $*p < 0.05$; $**p < 0.01$; $***p < 0.001$.

Site	Length (cm)	Weight (g)	Condition factor (*k*)[a]	Age (yr)	GSI[b]	Fecundity
Spawning males						
Jackfish Bay	36.9 ± 3.1 (100)**	741.4 ± 183.9 (100)	1.44 ± 0.08 (94)***	9.0 ± 3.4 (100)***		
Mountain Bay	38.2 ± 2.7 (99)	786.4 ± 172.6 (99)	1.39 ± 0.10 (99)	7.7 ± 3.9 (99)		
Spawning females						
Jackfish Bay	39.8 ± 2.9 (100)***	964.1 ± 222.5 (100)***	1.51 ± 0.12 (97)***	10.1 ± 3.8 (100)***	12.4 ± 3.6 (34)***	19602 ± 1380 (33)
Mountain Bay	41.9 ± 2.6 (101)	1067.7 ± 205.0 (101)	1.44 ± 0.09 (94)	8.4 ± 3.5 (101)	16.0 ± 2.7 (43)	21319 ± 9386 (39)
Summer males						
Jackfish Bay	39.4 ± 1.5 (42)***	964.5 ± 109.9 (41)*	1.59 ± 0.10 (41)***	9.0 ± 2.3 (42)		
Mountain Bay	41.5 ± 1.9 (52)	1016.6 ± 107.6 (51)	1.42 ± 0.10 (51)	10.6 ± 3.9 (52)		
Summer females						
Jackfish Bay	40.6 ± 2.2 (58)***	1043.6 ± 149.8 (56)**	1.56 ± 0.11 (56)***	9.4 ± 3.4 (58)*		
Mountain Bay	43.2 ± 2.4 (52)	1129.2 ± 147.2 (49)	1.40 ± 0.11 (49)	8.3 ± 2.9 (52)		

[a] $k = 100$ (wt/length^3).

[b] GSI = 100 × gonad wt/(body wt − gonad wt).

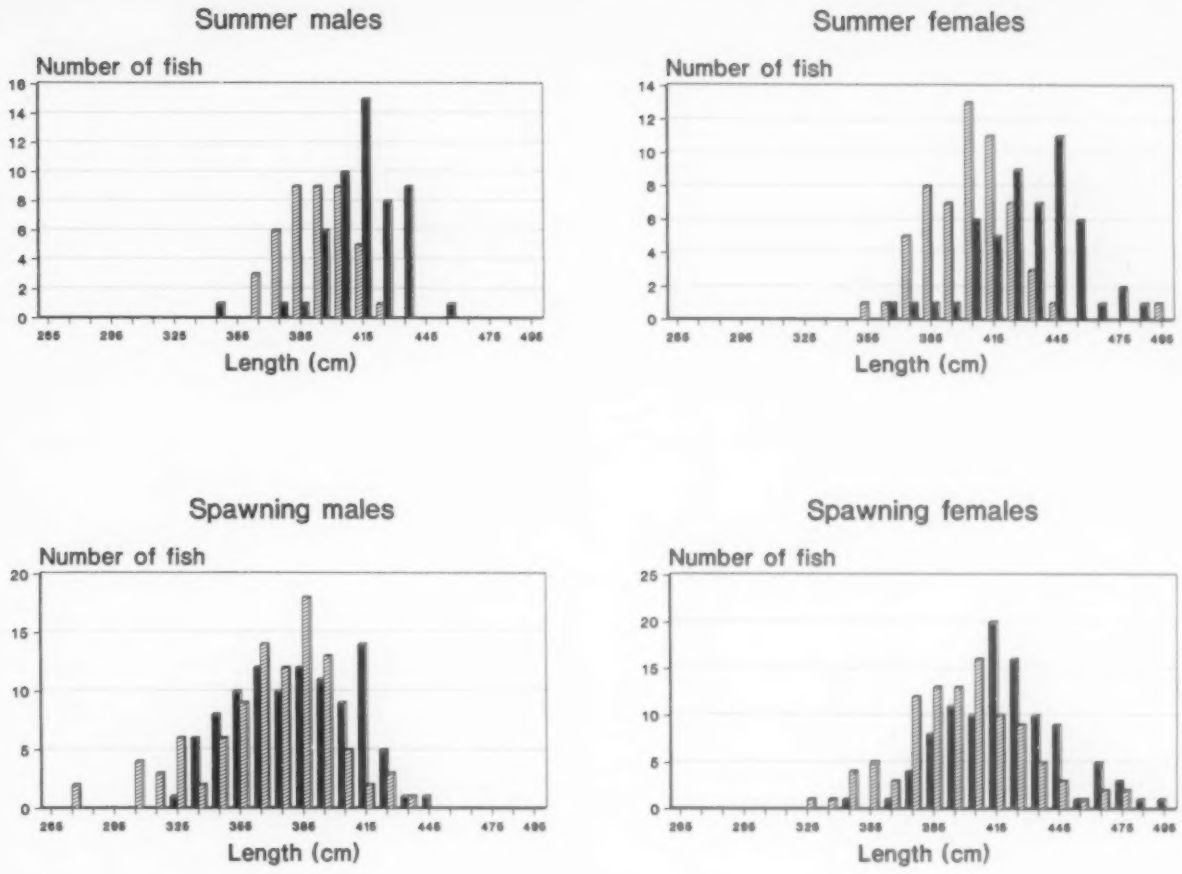


FIG. 2. Length–frequency distributions of white sucker males and females collected by hoop net during the spawning run and by gill net during the summer sampling period. Solid bars represent fish from the reference site and hatched bars represent BKME-exposed fish.

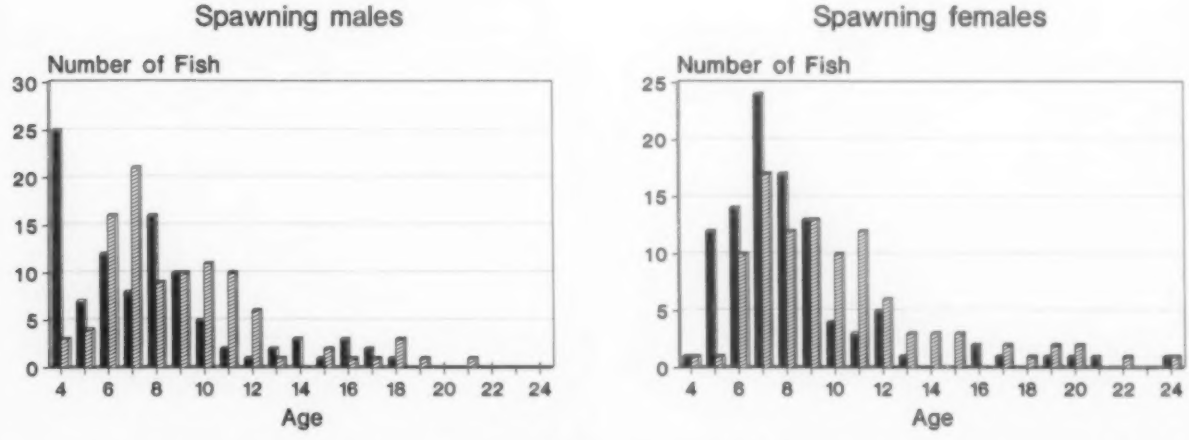


FIG. 3. Age distribution of white sucker males and females collected by hoop net during the spawning run. Solid bars represent fish from the reference site and hatched bars represent BKME-exposed fish.

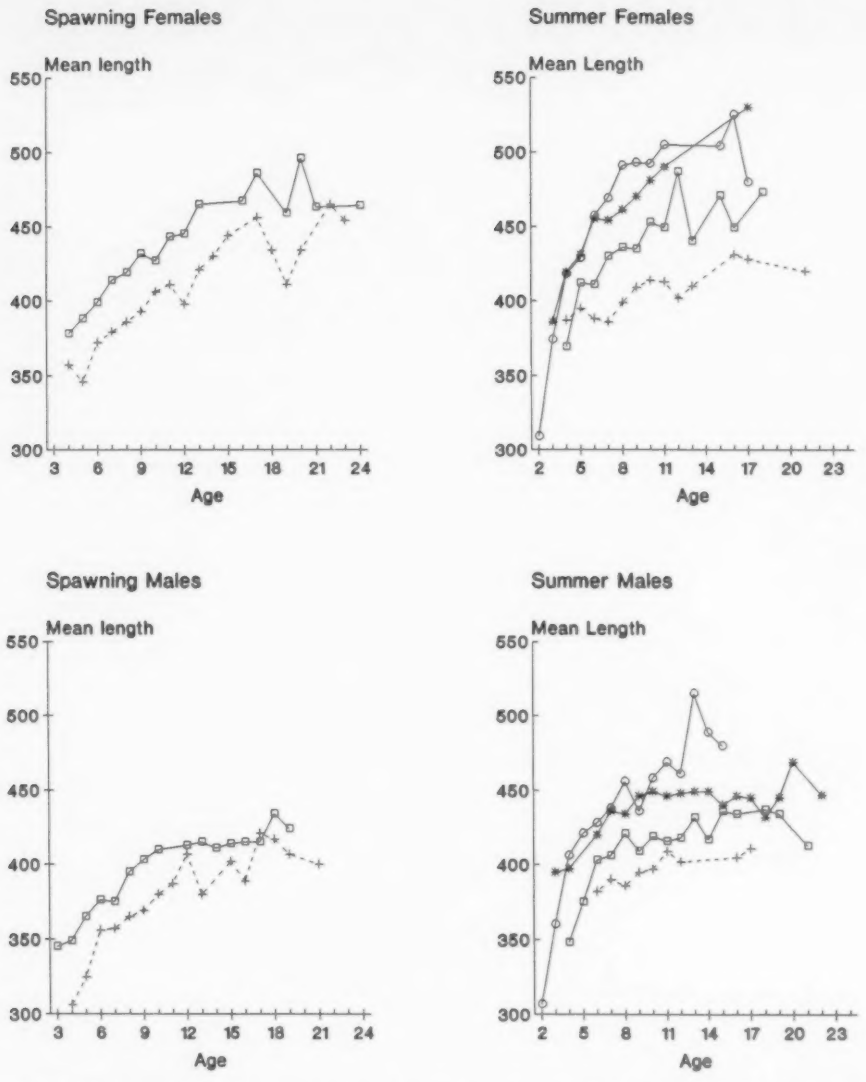


FIG. 4. Mean length of white sucker collected from reference sites (solid lines) and BKME site (broken lines) during the spawning season and during August 1988. Reference values for summer include white sucker from Mountain Bay (squares), Black Bay (asterisks), and Thunder Bay (circles), all located on Lake Superior. Spawning fish were collected by hoop net on the spawning beds, while summer fish were collected by single mesh sized gill nets (Thunder Bay and Black Bay data from I. R. Smith and C. B. Portt, unpubl. data).

0.01), and reached the age of maturity with lower fecundity (Fig. 5).

BKME-exposed spawning females showed lower GSI (Table 1; $p<0.001$) and lower gonadal weights ($p<0.001$; Fig. 6) than at a reference site. There was a highly significant difference in the slopes of ovarian weight versus adjusted body weight (body weight minus ovary weight) between sites ($p<0.001$), although mean fecundities were similar ($p = 0.112$). The lower ovarian weight at the BKME site arose due to differences in egg size. Fish collected from the BKME site did not show the increase in egg size in older fish which was noted at our reference site and in a previous study (Munkittrick and Dixon 1988). During the August collections, ovaries and testes were also observed to be much smaller at the BKME site than at the reference site, and the nuptial tubercles, a secondary sex characteristic, were not evident on male fish at the BKME site. All mature males examined in August at four other sites, including the reference site, showed significant tubercle development.

There was no significant difference in MFO activity towards PPO during the spawning run in either male or female white sucker (Table 3). However, fish collected during the summer sample showed increases in MFO activity towards both PPO and BaP substrates ($p<0.001$). Serum testosterone was lower in both male ($p = 0.008$) and female ($p<0.001$) white sucker at the BKME site, relative to Mountain Bay, and an additional

TABLE 2. Length, weight and age characteristics of the youngest 30 male and female white sucker collected during the spawning run. Values are reported as mean ± SEM (n). Statistical differences from reference site: $*p < 0.05$; $**p < 0.01$; $***p < 0.001$.

Site	Length (cm)	Weight (g)	Age (yr)
Males			
Jackfish Bay	34.8 ± 5.4	622.3 ± 29.7	5.9 ± 0.2***
Mountain Bay	35.2 ± 2.5	602.3 ± 16.2	4.1 ± 0.1
Females			
Jackfish Bay	37.4 ± 3.8***	810.0 ± 27.4**	6.5 ± 0.1***
Mountain Bay	39.6 ± 3.2	908.0 ± 22.9	5.6 ± 0.1

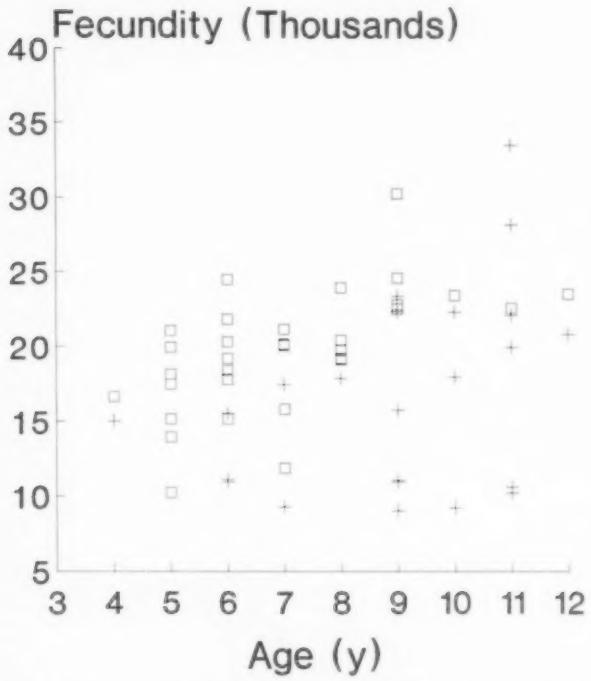


FIG. 5. Fecundity of white sucker from a BKME site (crosses) and a reference site (squares) versus age. Only younger fish are shown; there was no difference in mean fecundity between sites.

inland reference site at Loken Lake (see Munkittrick and Dixon 1988) (Table 4). Estradiol levels in females were not different ($p = 0.094$) between sites. There was no difference in the serum levels of T3 between sites ($p > 0.7$); female BKME fish showed higher levels of T4 ($p = 0.027$) than those of our reference site (Table 4).

Discussion

White sucker collected from a site receiving primary-treated BKME were older, grew more slowly, and exhibited a higher condition factor and lower reproductive commitments (ovarian weight and age-specific fecundity) than fish from comparable areas of Lake Superior. Changes in Jackfish Bay white sucker are consistent with a hypothesis of a disruption in metabolic capabilities and altered energy allocation (Hickie et al. 1989).

The growth rate of Jackfish Bay white sucker was lower than those at our reference site. The Mountain Bay site used as our reference site was the only unpopulated area on northern Lake Superior for which white sucker data were available. Additional information on growth rates is available from two other bays on northern Lake Superior (I. R. Smith, unpubl. data). In comparison with these other sites, the BKME fish also show a depressed growth rate, but comparisons between sites must be made carefully. The Thunder Bay site was located near the mouth of the Kaministiquia River (which is also impacted by pulp mill and other industrial dischargers), and the shift in age distribution towards younger fish and higher growth rates is probably attributable to the shallow water, lower fish densities, and higher water temperatures. Black Bay is subjected to an intense commercial fishery for white sucker, and the average age of fish captured in our 1990 spring collections was less than half of that at Mountain Bay or Jackfish Bay. It is probable that the increased growth rate is a result of exploitation and decreased fish density within Black Bay (type I response; Munkittrick and Dixon 1989b). It would appear that Mountain Bay fish would represent the most comparable reference site. Regardless of the comparability of sites, Jackfish Bay white sucker, with the observed increased condition factor, would be expected to show an increased growth rate and fecundity. The lower growth rate and decreased energetic commitment to reproduction suggest that there is a decreased ability of the fish to efficiently convert energy into somatic or reproductive tissue. Munkittrick and Dixon (1989b) previously described patterns of five population-level consequences of contaminant exposure which can be discriminated on the basis of changes in age, condition factor, and fecundity of the population. The response of the Jackfish Bay white sucker population does not fit with any of the five previously reported patterns (type I exploitation, II recruitment failure, III multiple stressors, IV food limitation, V niche shift). It appears that metabolic disruption could be associated with a sixth population response pattern (type VI) (Table 5).

The BKME-exposed fish also exhibited an increased age and decreased size to maturity, smaller gonads, lower fecundity (in young fish), an absence of secondary sex characteristics in males, and females failed to show an increase in egg size with age. The reduced steroid levels in white sucker from Jackfish Bay are consistent with the observed reductions. A similar increase in body fat and condition factor and decrease in gonadal size has been observed in lake whitefish (*Coregonus clupeaformis*) collected from Jackfish Bay in subsequent studies (McMaster et al. 1990). Abnormalities in carbohydrate metabolism have been previously associated with exposure to BKME from a Swedish pulp mill receiving only primary treatment (Andersson et al. 1988; Sandström et al. 1988). In both the Swedish studies, the changes in carbohydrate metabolism were coincident with increased activity of the hepatic MFO system.

The maximal degree of induction of AHH towards PPO (ninefold) was similar towards BaP (sevenfold). It has been shown previously that some MFO isozymes are increased by exposure to BKME, while others are decreased (Andersson et al. 1988). Numerous studies have shown that ethoxyresorufin-*o*-deethylase (EROD) and BaP-hydroxylase are induced in fish exposed to BKME (Oikari et al. 1984, 1985; Andersson et al. 1987; Larsson et al. 1988; Lindström-Seppa and Oikari 1989; Rogers et al. 1989). BKME, or its components, also affects phase II (conjugation) pathways, in some instances reducing hepatic activities of UDP-glucuronyl transferase

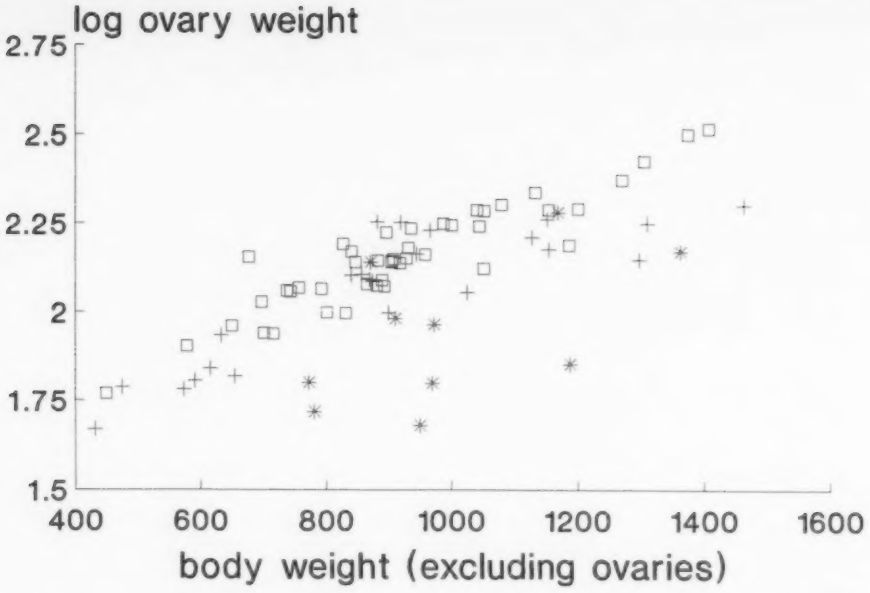


FIG. 6. Overy weight of female white sucker of different body weights. Body weight was standardized by removing ovarian weight from the comparison. The crosses represent fish from the BKME site and the squares represent fish from the control site. The asterisks represent female white sucker from the BKME site showing a gross liver lesion (presumptive tumour) during necropsy.

TABLE 3. MFO activity (mean ± SEM (*n*)) of PMS supernatant from homogenized livers of white sucker captured in the spring (spawning) and in midsummer from Jackfish Bay or its tributary (BKME site) and Mountain Bay or its tributary (reference site). Activity is reported as fluorescence units (FU) arising from the oxidation of PPO or BaP (Fu·mg protein^{-1}·min^{-1}). ***Significantly different from reference value ($p < 0.001$).

Site	Spring PPO (FU·mg^{-1}·min^{-1})	Summer PPO (FU·mg^{-1}·min^{-1})	BaP (FU·mg^{-1}·min^{-1})
Males			
Jackfish	4.7 ± 0.6 (9)	9.7 ± 1.4 (9)***	13.76 ± 2.97 (5)***
Mountain	4.5 ± 0.6 (11)	1.8 ± 0.2 (9)	1.98 ± 0.18 (3)
Females			
Jackfish	1.5 ± 0.2 (11)	11.5 ± 5.2 (8)***	8.78 ± 1.6 (5)***
Mountain	1.7 ± 0.3 (9)	1.3 ± 0.2 (8)	2.22 ± 0.55 (5)

TABLE 4. Hormone levels in blood sera of white sucker from a BKME site (Jackfish) and a reference site. Values are reported as mean ± SD (*n*). Statistical difference from reference site: *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$.

	Testosterone (pg·mL^{-1})	Estradiol (pg·mL^{-1})	T3 (ng·mL^{-1})	T4 (ng·mL^{-1})
Males				
Jackfish Bay	206 ± 55.1 (11)**	—	3.17 ± 2.84 (6)	33.5 ± 9.5 (8)
Mountain Bay	570 ± 134 (8)	—	6.44 ± 5.34 (5)	58.7 ± 24.6 (6)
Females				
Jackfish Bay	96 ± 11.4 (11)***	223.4 ± 24.2 (11)	3.58 ± 1.76 (10)	55.3 ± 9.5 (10)*
Mountain Bay	147 ± 47.9 (3)	557.9 ± 318 (3)	3.19 ± 1.76 (5)	17.5 ± 5.2 (5)
Loken Lake[a]	311 ± 32.3 (7)	432.7 ± 104.2 (7)[b]	3.19 ± 0.98 (8)	6.5 ± 2.6 (6)

[a]Another reference site located north of Lake Superior (see Munkittrick and Dixon 1988).
[b]$p = 0.094$.

TABLE 5. Generalized response patterns of fish to contaminant impacts. Metabolic disruption appears to be associated with a sixth pattern, distinct from those described earlier (Munkittrick and Dixon 1989a, 1989b).

Type	Generalized pattern	Mean age	Age distribution	Growth rate	Condition factor	Age at maturation	Fecundity	Egg size	Population size
I	Exploitation	−	Shift to younger	+	+	−	+	−/+[a]	−
II	Recruitment failure	+	Shift to older	0/+	0[b]	0	0	0	−
III	Multiple stressors	+	Shift to older	−	−	+	−	−/0	−
IV	Food limitation	0	No change	−	−	+	−	−	+
V	Niche shift	0	No change	−	0	+	−	−	−/0
VI	Metabolic disruption	0/−[c]	Shift to younger[d]	−	+	+	−[e]	−	0/−[a]

[a]Depending on degree of increase in food availability.
[b]0 signifies no increase or decrease.
[c]Exact magnitude and direction may vary; pattern not well described.
[d]In gillnet samples due to increased condition factor.
[e]Expressed as reproductive effort.

(UDPGT) (Oikari et al. 1984, 1985; Andersson et al. 1988; Tana 1988; Lindström-Seppa and Oikari 1989). Additional studies of hepatic biotransformation enzymes in white sucker have identified induction of MFO (BaP and PPO) and depression of UDPGT levels in additional Lake Superior locations affected by BKME (Smith et al. 1991).

There were seasonal changes in the activity of PPO metabolism, and the clear elevation evident during the summer sampling period was not seen during the spring spawning period. Although it is possible that the similarity between sites in the spring is related to the migration of fish to a BKME-free spawning site, AHH activity has been shown to decline with the onset of vitellogenesis in other fish species (Koivusaari et al. 1981; Walton et al. 1983; Lindström-Seppa 1985; Luxon et al. 1987). The factors regulating the seasonal changes in activity, and the potential for induction, are not known at this time.

The impact of changes in steroid levels, egg size, and fecundity on fertilization rate and recruitment is unknown at this time, although preliminary analysis has not shown a significant difference in fertility, survival, or larval deformities between sites (M. McMaster, D. G. Dixon, C. Portt, and K. R. Munkittrick, unpubl. data). There is no present understanding of how far steroid levels have to fall, or how long levels must be reduced, before biological consequences are induced. Johnson et al. (1988) found that fish at contaminated sites which were successful in entering vitellogenesis produced eggs normally. Other workers have shown a negative correlation between maternal hepatic AHH activity (associated with PAH and PCB exposure) and vitellogenesis, percent viable eggs, fertilization success, and embryological success; however, such correlations were not always evident (Spies et al. 1988; Spies and Rice 1988).

It has not been established whether MFO enzymes are directly linked to decreased levels of steroids, or which specific hepatic enzymes and inducers may be involved. Since steroids are a natural substrate for MFO enzymes (Payne et al. 1987), there is the possibility that high levels of MFO activity may result in a decrease in circulating steroid levels. However, the major inducible AHH isozymes associated with contaminant exposure do not significantly metabolize steroids in vitro (Stegeman and Kloepper-Sams 1987), and the induction of EROD by β-napthoflavone does not induce estradiol metabolism (Snowberger and Stegeman 1987). The cause of the decreased gonadal size may not be directly attributable to the lower steroid levels. White sucker exposed to BKME show an abnormal incidence of hepatic preneoplasia and neoplasia in Jackfish Bay (I. R. Smith, unpubl. data), as well as in Thunder Bay (also on Lake Superior; Smith and Rokosh 1989). The presence of gross hepatic lesions at necropsy (many have been confirmed histologically; I. R. Smith, unpubl. data) correlated with reduced ovarian weight (Fig. 6). Correlations between high levels of organic contaminants and hepatic lesions have also been reported elsewhere (Krahn et al. 1986; Collier and Varanasi 1988; Johnson et al. 1988).

The impacts of pulp mills on aquatic environments are of considerable concern and importance. White sucker collected from a site receiving primary-treated BKME effluent showed abnormalities in growth rate, reproductive development, fecundity with age and age to maturation, secondary sexual characteristics, gonadal size, and egg size, which correlated with decreases in serum levels of estradiol and testosterone, and with increases in the activity of hepatic MFO enzymes. There are no industrial inputs to Jackfish Bay other than >70 000 L primary-treated effluent·min^{-1} from a bleached kraft mill. Although further research is ongoing in an attempt to link exposure levels and biological effects, we found clear evidence of steroid abnormalities downstream of a bleached kraft pulp mill and confirmed Scandinavian studies describing impacts of pulp mills on growth and gonadal development (see introduction for references).

Acknowledgements

Part of this work was conducted while the senior author (K.R.M.) was employed with E.V.S. Consultants, North Vancouver, B.C. Financial assistance was also provided by Natural Sciences and Engineering Research Council of Canada funding to G.V.D.K. and to Dr. John Leatherland (Department of Zoology, University of Guelph, Guelph, Ont.). Laboratory assistance for thyroid hormone analysis was provided by Peter Flett and Lucy Lin (Department of Zoology, University of Guelph). Janine Clemens (Ontario Ministry of Environment, Rexdale, Ont.) provided assistance with MFO analyses. Field collections were supervised by Leo Marchand (Marchand and Maye Fisheries) and assisted by Steve King (C. Portt and Associates). The

assistance of Linda Melnyk-Ferguson (Ontario Ministry of Natural Resources, Terrace Bay, Ont.) and Lorne Townes (Ontario Ministry of Natural Resources, Nipigon, Ont.) is gratefully acknowledged.

References

ANDERSSON, T. E., B.-E. BENGTSSON, L. FÖRLIN, J. HÄRDIG, AND Å. LARSSON. 1987. Long term effects of kraft mill effluents on carbohydrate metabolism and hepatic xenobiotic biotransformation enzymes in fish. Ecotoxicol. Environ. Safety. 13: 53–60.

ANDERSSON, T., L. FÖRLIN, J. HÄRDIG AND Å. LARSSON. 1988. Physiological disturbances in fish living in coastal waters polluted with bleached kraft mill effluents. Can. J. Fish. Aquat. Sci. 45: 1525–1536.

BÖHLING, P., R. HUDD, H. LEHTONEN, P. KARÅS, E. NEUMAN, AND G. THORESSON. 1991. Variations in year-class strength of different perch (*Perca fluviatilis*) populations in the Baltic Sea with special reference to temperature and pollution. Can. J. Fish. Aquat. Sci. 48. (In press)

BRADFORD, M. M. 1976. A rapid and sensitive method for the quantitation of microgram quantities of protein utilizing the principle of protein dye-binding. Anal. Biochem 72: 248–254.

BURKE, M. G., AND J. F. LEATHERLAND. 1983. Seasonal changes in serum thyroid hormone levels of the feral brown bullhead, *Ictalurus nebulosus* LeSueur. J. Fish Biol. 23: 585–593.

COLLIER, T. K., AND U. VARANASI. 1988. Xenobiotic metabolizing enzymes in two species of benthic fish showing different prevalences of hepatic neoplasms in contaminated areas. Mar. Environ. Res. 24: 113.

FLOOD, K., D. HOLLINGER, M. THOMSON, W. WAGER, AND W. BANAS. 1986. Jackfish Bay: acute lethality and chlorophenol bioconcentration in fish exposed to a bleached kraft mill effluent (BKME) plume. Ontario Ministry of Environment Report, Rexdale, Ont. 44 p.

HICKIE, B. E., D. G. DIXON, AND J. F. LEATHERLAND. 1989. The influence of dietary carbohydrate:lipid ratio on the chronic toxicity of sodium pentachlorophenate to rainbow trout (*Salmo gairdneri* Richardson). Fish Biochem. Physiol. 6: 175–185.

INTERNATIONAL JOINT COMMISSION (IJC). 1989. 1989 report on Great Lakes water quality. Appendix A: Progress in developing and implementing remedial action plans for areas of concern in the Great Lakes Basin. Great Lakes Water Quality Board, Report to the International Joint Commission, Hamilton, Ontario, October 1989. 196 p.

JOHNSON, L. L., E. CASILLAS, T. K. COLLIER, B. B. MCCAIN, AND U. VARANASI. 1988. Contaminant effects on ovarian development in English sole (*Parophrys vetulus*) from Puget Sound, Washington. Can. J. Fish. Aquat. Sci. 45: 2133–2146.

KARÅS, P., E. NEUMAN, AND O. SANDSTRÖM. 1991. Effects of a pulp mill effluent on the population dynamics of perch, *Perca fluviatilis*. Can. J. Fish. Aquat. Sci. 48: 28–34.

KOIVUSAARI, U., M. HARRI, AND O. HANNINEN. 1981. Seasonal variation of hepatic biotransformation in female and male rainbow trout (*Salmo gairdneri*). Comp. Biochem. Physiol. 70C: 149–157.

KRAHN, M. M., L. D. RHODES, M. S. MEYERS, L. K. MOORE, W. D. MACLEOD, JR., AND D. C. MALINS. 1986. Associations between metabolites of aromatic compounds in bile and the occurrence of hepatic lesions in English sole (*Parophrys vetulus*) from Puget Sound, Washington. Arch. Environ. Contam. Toxicol. 15: 61–67.

LARSSON, L., T. ANDERSSON, L. FÖRLIN, AND J. HÄRDIG. 1988. Physiological disturbances in fish exposed to bleached kraft mill effluents. Water Sci. Technol. 20: 67–76.

LINDSTRÖM-SEPPA, P. 1985. Seasonal variation of the xenobiotic metabolizing enzyme activities in the liver of male and female vendace (*Coregonus albula* L.). Aquat. Toxicol. 6: 323–331.

LINDSTRÖM-SEPPA, P., AND A. OIKARI. 1989. Biotransformation and other physiological responses in whitefish caged in a lake receiving pulp and paper effluents. Ecotoxicol. Environ. Safety 18: 191–203.

LUXON, L., P. V. HODSON, AND U. BORGMANN. 1987. Hepatic aryl hydrocarbon hydroxylase activity of lake trout (*Salvelinus namaycush*) as an indicator of organic pollution. Environ. Toxicol. Chem. 6: 649–657.

MCLEAY, D. 1987. Aquatic toxicity of pulp and paper mill effluent: a review. EPA 4/PF/1, Environment Canada, Ottawa, Ont.

MCMASTER, M. E., D. G. DIXON, K. R. MUNKITTRICK, C. PORTT, G. J. VAN DER KRAAK, I. R. SMITH, AND D. ROKOSH. 1990. Impact of bleached kraft mill effluent (BKME) on fish populations near Terrace Bay, Ontario. Proc. Ont. Minist. Environ. Tech. Transfer Workshop, Nov. 19–20, 1990, Toronto, Session B (Water Quality Research). Vol. 1: 295–301.

MUNKITTRICK, K. R., AND D. G. DIXON. 1988. Growth, fecundity and energy stores of white sucker (*Catostomus commersoni*) exposed to elevations of copper and zinc. Can. J. Fish. Aquat. Sci. 45: 1355–1365.

1989a. Use of white sucker (*Catostomus commersoni*) populations to assess the health of aquatic ecosystems exposed to low-level contaminant stress. Can. J. Fish. Aquat. Sci. 46: 1455–1462.

1989b. A holistic approach to ecosystem health assessment using fish population characteristics. *In* M. Munawar, G. Dixon, C. I. Mayfield, and M. H. Sadar [ed.] Environmental bioassay techniques and their application. Kluwer Academic Publishers, The Netherlands. Hydrobiologia 188/189: 123–135.

NEBERT, D. W., AND G. V. GELBOIN. 1968. Substrate-inducible microsomal aryl hydroxylase in mammalian cell culture. J. Biol. Chem. 243: 6242–6249.

NEUMAN, E., AND P. KARÅS. 1988. Effects of pulp mill effluent on a Baltic coastal fish community. Water Sci. Technol. 20: 95–106.

OIKARI, A., B. HOLMBOLM, E. ANAS, M. MIILUNPALO, G. KRUZYNSKI, AND M. CASTREN. 1985. Ecotoxicological aspects of pulp and paper mill effluents discharged to an inland water system: distribution in water, and toxicant residues and physiological effects in caged fish (*Salmo gairdneri*). Aquat. Toxicol. 6: 219–239.

OIKARI, A., T. NAKARI, AND B. HOLMBOLM. 1984. Sublethal actions of simulated kraft pulp mill effluents (KME) in *Salmo gairdneri*: residues of toxicants, and effects on blood and liver. Ann. Zool. Fenn. 21: 45–53.

PAYNE, J. F., L. L. FANCY, A. D. RAHIMTULA, AND E. L. PORTER. 1987. Review and perspective on the use of mixed-function oxygenase enzymes in biological monitoring. Comp. Biochem. Physiol. 86C: 233–245.

ROGERS, H., C. D. LEVINGS, W. L. LOCKHART, AND R. J. NORSTROM. 1989. Observations on overwintering juvenile chinook salmon (*Oncorhynchus tshawytscha*) exposed to bleached kraft mill effluent in the Upper Fraser River, British Columbia. Chemosphere 19: 1853–1868.

SANDSTRÖM, O., E. NEUMAN, AND P. KARÅS. 1988. Effects of a bleached pulp mill effluent on growth and gonad function in Baltic coastal fish. Water Sci. Technol. 20: 107–118.

SANDSTRÖM, O., AND G. THORESSON. 1988. Mortality in perch populations in a Baltic pulp mill effluent area. Mar. Pollut. Bull. 19: 564–567.

SHERMAN, R. K., R. E. CLEMENT, AND C. TASHIRO. 1990. The distribution of polychlorinated dibenzo-*p*-dioxins and dibenzofurans in Jackfish Bay, Lake Superior, in relation to a kraft mill effluent. Chemosphere 20: 1641–1648.

SMITH, I. R., C. PORTT, AND D. A. ROKOSH. 1991. Hepatic mixed function oxidases are induced in populations of white sucker, *Catostomus commersoni*, from areas of Lake Superior and the St. Mary's River. J. Great Lakes Res. (In press)

SMITH, I. R., AND D. A. ROKOSH. 1989. An epidemiological study of a white sucker (*Catostomus commersoni*) population inhabiting the Kaministiquia River, Thunder Bay, Ontario. Abstr. 262, 10th Annual Meeting Soc. Environ. Toxicol. Chem., Oct. 28 – Nov. 2 1989, Toronto, Ont.

SNOWBERGER, E. A., AND J. J. STEGEMAN. 1987. Patterns and regulation of estradiol metabolism by hepatic microsomes from two species of marine teleosts. Gen. Comp. Endocrinol. 66: 256–265.

SPIES, R. B., AND D. W. RICE, JR. 1988. Effects of organic contaminants on reproduction of starry flounder, *Platichthys stellatus* in San Francisco Bay. II. Reproductive success of fish captured in San Francisco Bay and spawned in the laboratory. Mar. Biol. 98: 191–200.

SPIES, R. B., D. W. RICE, JR., AND J. FELTON. 1988. Effects of organic contaminants on reproduction of starry flounder, *Platichthys stellatus* in San Francisco Bay. I. Hepatic contamination and mixed-function oxidase (MFO) activity during the reproductive season. Mar. Biol. 98: 181–189.

SPRAGUE, J. B., AND A. G. COLODEY. 1989. Toxicity to aquatic organisms of organochlorine substances in kraft mill effluents. Report for Renewable Resources, Extraction and Processing Division, Industrial Programs Branch, Conservation and Protection, Environment Canada, Ottawa, Ont., June 1989. 53 p.

STEGEMAN, J. J., AND P. J. KLOEPPER-SAMS. 1987. Cytochrome P-450 isozymes and monooxygenase activity in aquatic animals. Environ. Health Perspect. 71: 87–95.

TANA, J. J. 1988. Sublethal effects of chlorinated phenols and resin acids on rainbow trout (*Salmo gairdneri*). Water Sci. Technol. 20: 77–85.

VAN DER KRAAK, G., H. M. DYE, AND E. M. DONALDSON. 1984. Effects of LHRH and Des Gly^{10} (D-Ala^{6}) LHRH-ethylamide on plasma sex steroid profiles in adult female coho salmon (*Oncorhynchus kisutch*). Gen. Comp. Endocrinol. 55: 35–45.

VAN DER KRAAK, G., P. M. ROSENBLUM, AND R. E. PETER. 1990. Growth hormone-dependent potentiation of gonadotropin-stimulated steroid production by ovarian follicles of the goldfish. Gen. Comp. Endocrinol. 79: 233–239.

WALTON, D. G., L. L. FANCEY, J. M. GREEN, J. W. KICENIUK, AND W. R. PENROSE. 1983. Seasonal changes in aryl hydrocarbon hydroxylase activity of a marine fish *Tautogolabrus adspersus* (Walbaum) with and without petroleum exposure. Comp. Biochem. Physiol. 76C: 247–253.

Distribution and Dispersal of the Zebra Mussel (*Dreissena polymorpha*) in the Great Lakes Region[1]

Ronald W. Griffiths

Ministry of the Environment, Water Resources Assessment Unit, 985 Adelaide St. South, London, Ont. N6E 1V3, Canada

Donald W. Schloesser

U.S. Fish and Wildlife Service, National Fisheries Research Center - Great Lakes, 1451 Green Road, Ann Arbor, MI 48105, USA

Joseph H. Leach

Ministry of Natural Resources, Lake Erie Fisheries Station, Wheatley, Ont. N0P 2P0, Canada

and William P. Kovalak

Detroit Edison Company, 2000 Second Avenue, Detroit, MI 48226, USA

Griffiths, R. W., D. W. Schloesser, J. H. Leach, and W. P. Kovalak. 1991. Distribution and dispersal of the zebra mussel (*Dreissena polymorpha*) in the Great Lakes region. Can. J. Fish. Aquat. Sci. 48: 1381–1388.

Dreissena polymorpha (Pallas), a small mussel common throughout most of Europe, was discovered in June of 1988 in the southern part of Lake St. Clair. Length–frequency analyses of populations from the Great Lakes and review of historical benthic studies suggest that the mussel was introduced into Lake St. Clair in late 1986, probably as a result of the discharge of ballast water from an ocean-crossing vessel. Following the 1990 reproductive season, *Dreissena* populations ranged from the head of the St. Clair River, through Lake St. Clair, the Detroit River, Lake Erie, the Welland Canal, and the Niagara River to the western basin and southern shoreline of Lake Ontario. Isolated populations were found in the St. Lawrence River and in harbours in Lakes Huron, Michigan, and Superior. The rapid dispersal of this organism has resulted from its high fecundity, pelagic larval stage, bysso-pelagic drifting ability of juveniles, and human activities associated with commercial shipping, fishing, and boating (research and pleasure). Virtually any waterbody that can be reached by boaters and fisherman within a few days travel of the lower Great Lakes, particularly Lake Erie, seems to be at risk of being invaded by this nuisance species.

Le *Dreissena polymorpha* (Pallas), une petite moule commune dans la plus grande partie de l'Europe, a été découverte en juin 1988 dans la partie sud du lac Ste-Claire. Des analyses des fréquences de longueurs des populations des Grands lacs et un examen des études benthiques historiques suggèrent que cette moule a été introduite dans le lac Ste-Claire vers la fin de 1986, probablement à la suite des déversements d'eau de ballast d'un navire océanique. Après la saison de reproduction de 1990, les populations de *Dreissena* étaient observées à la tête de la rivière Ste-Claire, en passant par le lac Ste-Claire, la rivière Détroit, le lac Érié, le canal Welland et la rivière Niagara, jusqu'au bassin ouest et à la rive sud du lac Ontario. On a observé des populations isolées dans le fleuve St-Laurent et dans des ports des lacs Huron, Michigan et Supérieur. La dispersion rapide de cet organisme est due à sa grande fécondité, au stade de larves pélagiques, à la capacité de dérive bysso-pélagique des juvéniles et aux activités humaines associées à la navigation commerciale, à la pêche et à la navigation de recherche et de plaisance. À peu près toutes les étendues d'eau à moins de quelques jours de distance des Grands Lacs inférieurs, et plus particulièrement du lac Érié, qui peuvent être visitées par les bateaux et les pêcheurs, semblent être menacées d'invasion par cette espèce nuisible.

Received August 29, 1990
Accepted April 9, 1991
(JA707)

Reçu le 29 août 1990
Accepté le 9 avril 1991

The zebra mussel, *Dreissena polymorpha* (Pallas), a small bivalve common throughout most of Europe and historically native to the Black, Caspian, and Azov seas (Stanczykowska 1977), was discovered in June of 1988 in the southern part of Lake St. Clair (Hebert et al. 1989). Its introduction to North America probably resulted from an ocean-crossing vessel discharging freshwater ballast that contained free-swimming larvae of the mussel (i.e. veligers), a mechanism that has been implicated for the recent discovery of several exotic species in the Great Lakes (Schormann et al. 1990; Berg and Garton 1988; Schloesser et al. 1986; Barton and Griffiths 1984). The exact date and location of this introduction are unknown. However, extensive benthic surveys conducted in the Detroit River in 1983 and 1984, Lake St. Clair in 1983, 1984, and 1986, and St. Clair River in 1983, 1984, and 1985 failed to collect a single specimen (Hudson et al. 1986; Griffiths 1987, 1989b; Nalepa and Gauvin 1988). Since it can be pre-

[1]Contribution No. 760 at the National Fisheries Research Center - Great Lakes.

sumed to have been in Lake St. Clair before 1988, as demonstrated by the length–frequency distribution of mussel shells collected in August of 1988 (Hebert et al. 1989), the introduction most likely occurred in 1986 or 1987. *Dreissena* has spread rapidly since its introduction; in the late summer of 1989, it was found from the mouth of the St. Clair River, throughout the southern half of Lake St. Clair, to the eastern extreme of Lake Erie (Griffiths et al. 1989; Hebert et al. 1991).

In Europe, *Dreissena* is a well-known biofouling organism that can disrupt the operations of water treatment and electrical generating facilities (Clarke 1952; Greenshields and Ridley 1957; Shtegman 1964; Morton 1979; Afanas'yev and Protasov 1987), negatively affect native species populations (Sebestyen 1938; Arter 1989), and alter the energy and nutrient flow of aquatic ecosystems (Stanczykowska et al. 1976; Stanczykowska 1977; Shevtsova and Kharchenko 1981; Stanczykowska and Planter 1985; Kharchenko and Lyashenko 1985; Hamburger et al. 1990). Some of these same impacts have recently been observed in the Great Lakes (Griffiths et al. 1989; Hebert et al. 1989; Hebert et al. 1991).

Given its potential for widespread, rapid dispersal and considering its potential impact on aquatic systems and cost to industry, it is important to gain a better understanding of the dispersal dynamics and likely invasion routes of this nuisance species. We have attempted to do this by determining the current and historical spatial distribution of *Dreissena* within the Great Lakes and then elucidating its dispersal rate, mechanisms, and invasion routes from these patterns and knowledge of its life history and environmental requirements.

Methods

The prediscovery (i.e. before 1988) spatial distribution of *Dreissena* was estimated from length–frequency analysis of mussel populations, surface current patterns, and a review of historical benthic invertebrate studies. Mussels for length–frequency analysis were collected from 16 sites: 9 benthic, 5 industrial, and 2 pelagic (i.e. objects in the water column) in Lake St. Clair and Lake Erie from September 1989 to May 1990 (Fig. 1). An additional sample collected in February of 1989 from the electrical generating plant in Monroe, Michigan, was also available. At benthic sites, all animals on a specific substrate (e.g. rock, unionid shell) or obtained from several Ekman grabs were retained; at industrial sites, all animals from a specific area of an intake, inlet channel wall, or artifical substrate were collected; and at pelagic sites, all animals from several areas on a buoy or leg of a gas platform were obtained. The animals then were placed in a jar and preserved with alcohol or 10% formalin. The length of individuals greater than 2 mm was measured to the nearest whole millimetre.

The postdiscovery (i.e. 1988–90) spatial distribution of *Dreissena* in the Great Lakes basin was summarized at the end of each calender year by mapping the location where macroscopically visible individuals had been observed from periodic surveys of beaches, nearshore areas, water treatment plants, electrical generating facilities, industrial plants, navigation buoys, and inland lakes and rivers. Since *Dreissena* only reproduces when water temperature exceeds 12°C (Sprung 1987; L'vov 1980; Stanczykowska 1977; Kornobis 1977), which corresponds roughly to the period of June through September in the lower Great Lakes, all observations recorded from January to May were assumed to represent the cohort of the previous year and therefore posted to the map of the previous year.

Results

Length–Frequency Distributions

Frequency distributions of shell lengths suggest that *Dreissena* populations in Lake St. Clair and Lake Erie were composed of one to possibly four cohorts (Fig. 2 and 3). Single cohorts of small individuals were evident at sites in the easternmost part of Lake Erie: Nanticoke, Dunkirk, and Presque Isle. Settled mussels less than 3 mm in length were first noted at the electrical generating plant at Nanticoke in August of 1989.

Two cohorts were found attached to a gas production platform located 10 km south of Clear Creek (42°28′21″N, 80°32′14″W). Young mussels (<12 mm) were present on the support legs from 6.5 to 20 m depth. Large mussels (17–26 mm) were found only on the pad of the structure (21 m depth). Because the platform is towed to shore every autumn for winter storage, only the pad remains submerged throughout the year. Mussels on the legs of the structure thus represent animals that settled during the 1989 season.

In benthic habitats in the western half of Lake Erie, three cohorts were evident west of Rondeau Bay, while possibly two cohorts were indicated in the east end of the bay (Fig. 2). Around Pelee Island, two cohorts were evident at Chickenolee shoal whereas three cohorts were possibly present at Hen Island shoal and Little Chicken Island shoal, although the number of large animals (>10 mm) collected at the latter site was low. The maximum density of animals on the shoals was about 30 000·m^{-2}. Finally, two cohorts were evident near Little Sister Island.

Two cohorts were apparent at the electrical generating plant in Monroe in February of 1989, while three cohorts were probably present in January of 1990, with the largest animals (23–28 mm) representing the 9–21 mm cohort in February of 1989 (Fig. 3). The maximum density of mussels found in the intake canal was 700 000·m^{-2}.

At least two cohorts were present at the electrical generating plant near Cleveland (Fig. 3); the low number of large animals (17–29 mm) makes it difficult to further divide this group into separate cohorts. However, the size range of mussels was similar to that at Monroe in January of 1990 (Fig. 3), suggesting that the large individuals may represent two cohorts.

In Lake St. Clair, three cohorts were apparent at the benthic site located east of Peche Island (density about 500·m^{-2}) and offshore of the town of Ruscom, near where the first zebra mussel was found in June of 1988 (S. Gutschi, Ministry of Environment, London, Ont., pers. comm.), although the abundance of large specimens was very low (Fig. 2). Three cohorts may also have been present in the intake of the water treatment plant that supplies the town of Tilbury (density about 140 000·m^{-2}), although the somewhat even distribution of shell lengths makes it difficult to precisely separate each cohort (Fig. 3). Similarly, three cohorts appeared to be present on a marker buoy located east of Peche Island (42°21′66″N, 82°50′09″W). However, these animals had to have settled on the buoy during the 1989 season, since it had only been in the water for 5 mo (May to October).

Among benthic sites, the largest mussels (25–30 mm) were confined to southern Lake St. Clair and western Lake Erie, west of Pelee Island (Fig. 2). These individuals possibly were the oldest in the lakes and may have represented an additional cohort at these sites. Furthermore, the largest mussels found at the industrial sites were those in the Monroe and Cleveland

FIG. 1. Location of sampling sites where zebra mussels were collected for length–frequency analysis. Solid circles indicate benthic sites, stars indicate industrial sites, and open circles indicate pelagic sites (i.e. objects in the water column).

facilities (Fig. 3), which helps support the concept that the oldest populations occurred in the southwestern areas of Lake St. Clair and Lake Erie.

Discussion

Population Age Structure

The length–frequency distributions of shell lengths from the benthic sites were similar to those reported for *Dreissena* in European lakes (Hamburger et al. 1990; Bij de Vaate 1991; Lewandowski 1983; Walz 1973, 1978b; Stanczykowska 1977; Wiktor 1963). The reported life span for *Dreissena* from these waterbodies ranged from 3 to 9 yr, with 4–6 yr commonly observed (Hamburger et al. 1990; Morton 1979; Kornobis 1977; Stanczykowska 1977). Since a single cohort is produced each year (Walz 1978a; Kornobis 1977; Stanczykowska 1977), frequency modes can be used to identify year-classes (e.g. Walz 1973; Morton 1969).

The direct interpretation of length–frequency distributions in terms of population age structure, however, is confounded by several factors: (a) poor survival of individuals in nearshore areas over the winter season, (b) movement of juvenile and adult individuals; (c) influence of water currents on growth rate, and (d) variability in cohort growth rates between years. The nearshore population of *Dreissena* in Rondeau Bay may not represent the total population age structure in the area because few, if any, individuals in nearshore areas survive the winter. At Leamington Harbour, on the north shore of Lake Erie just west of Pt. Pelee, mussels in nearshore areas occurred at densities of up to 5000 individuals·m^{-2} in November of 1988 but were completely absent the following spring. Although European investigators have suggested that this phenomenon represents a downward migration of individuals from the nearshore zone (Ehrenberg 1957; Berg 1938; Lundbeck 1926), it is more likely that autumn storms and the scouring action of ice during the winter dislodge and destroy the population. Shells from this population probably made up a large proportion of those washed up along Lake Erie beaches in the autumn of 1989, producing a band of shells up to 30 cm deep.

The older cohorts on the marker buoy in Lake St. Clair (Fig. 3) probably represented juvenile and adult animals from the local area that colonized the buoy either by using a byssal drag line and riding upwelling currents or by simply crawling up the attached anchor line. Juvenile zebra mussels use byssal threads as a means to climb over objects (von Winkle 1970; Young and Campbell 1968) and as a means to drift (personal observation), a behavior also reported for marine mussels (Lane et al. 1982) and *Corbicula* (Prezant and Chalermwat 1984). Although adults tend to remain more sessile, they can dissolve their threads (Lewandowski 1976) and then use new ones to assist their movement, leaving the old byssus behind. We have noted individuals as large as 22 mm conduct this behavior in aquaria.

The length–frequency distributions suggest that a 7–9 mm individual from the benthic population located east of Peche Island or west of Rondeau was probably 1 yr of age (Fig. 2) whereas a similar sized individual on the buoy in Lake St. Clair or the water intake trash bars of the electrical generating plant

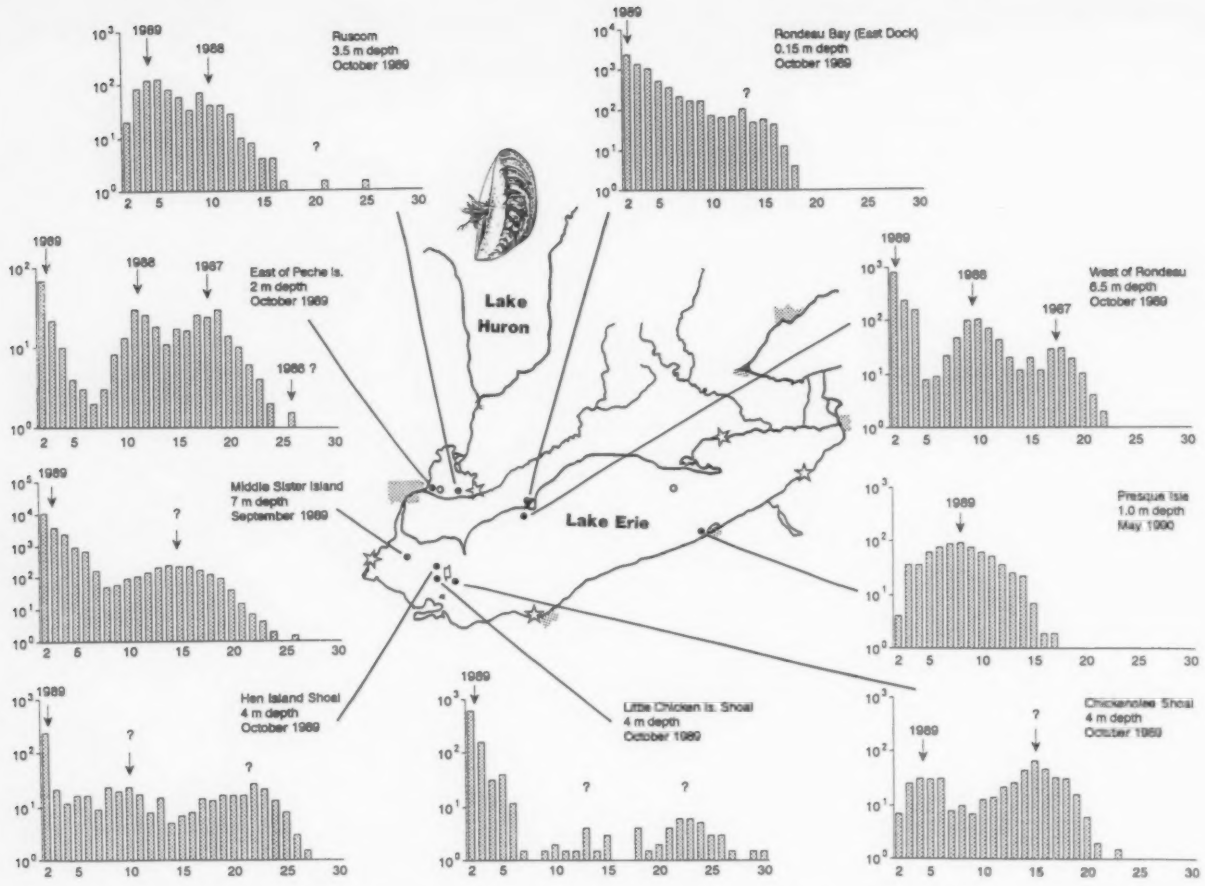


FIG. 2. Length–frequency histograms of *D. polymorpha* from nine benthic sites in the Great Lakes. Shell length (mm) is marked on the abscissa and number of animals is represented on the ordinate. Location, sampling depth, and date are noted on each histogram. Arrows indicate modes (= cohorts). Data above arrows indicates the year of settlement for the cohort.

near Cleveland was likely less than 1 yr of age (Fig. 3). Thus, the age structure of a population cannot be determined simply from the size of the largest individual because growth is influenced by water currents (Jenner and Mommen 1985; Kornobis 1977; Stanczykowska 1977). Kachanova (1962) showed that the growth of *Dreissena* in water channels was twice that seen in reservoirs. Similarly, Bij de Vaate (1991) found that surface currents doubled the growth of young-of-the-year individuals on a buoy relative to those on the bottom of the lake. Mussels sampled from an environmentally homogeneous site, therefore, should produce well-defined length–frequency modes from which the age structure of the population can be determined. In contrast, mussels collected from an environmentally heterogeneous area or several environmentally homogeneous sites should produce poorly defined modes, difficult to interprete in terms of age structure.

The cohort with a modal value of about 15 mm observed at Middle Sister Island and Chickenolee Shoal probably represented two merged cohorts with modal values similar to those west of Rondeau and east of Peche Island (Fig. 2). Young cohorts have been shown to overgrow older cohorts, thus making it difficult to distinguish them from a length–frequency distribution (Bij de Vaate 1991). This phenomenon was evident at the electrical generating plant in Monroe, where cohorts could be distinguished in February of 1989, but not in January of 1990 (Fig. 3).

Our interpretation of the length–frequency distributions, therefore, is that a single year-class, individuals of the 1989 cohort, was present at Nanticoke, Dunkirk, and Presque Isle at the end of 1989, at least two year-classes at the gas platform site in the central basin of Lake Erie, in Rondeau Bay, and at Cleveland, and three year-classes west of Rondeau Bay and at Monroe. Three year-classes were also present at the benthic sites in southern Lake St. Clair and in Lake Erie west of Pelee Island, with the possibility of a fourth. The length–frequency distributions of the populations east of Peche Island and west of Rondeau Bay match well with those from central European lakes (Bij de Vaate 1991; Lewandowski 1983; Walz 1973, 1978b). Using the growth increment equation of Bij de Vaate (1991), individuals with a shell length of 2 mm would grow to 11, 18, and 22 mm in each subsequent year. The congruence between these predicted lengths and the modal values of the two Great Lakes populations above, 2 mm for the 1989 cohort, 10–11 mm for the 1988 cohort, and 18–19 mm for the 1987 cohort, suggests that the modal value for a 1986 cohort would be 22 mm. Mussel populations at the benthic sites in Lake St. Clair and in Lake Erie west of Pelee Island all had individuals exceeding a length of 22 mm, suggesting that a 1986 cohort

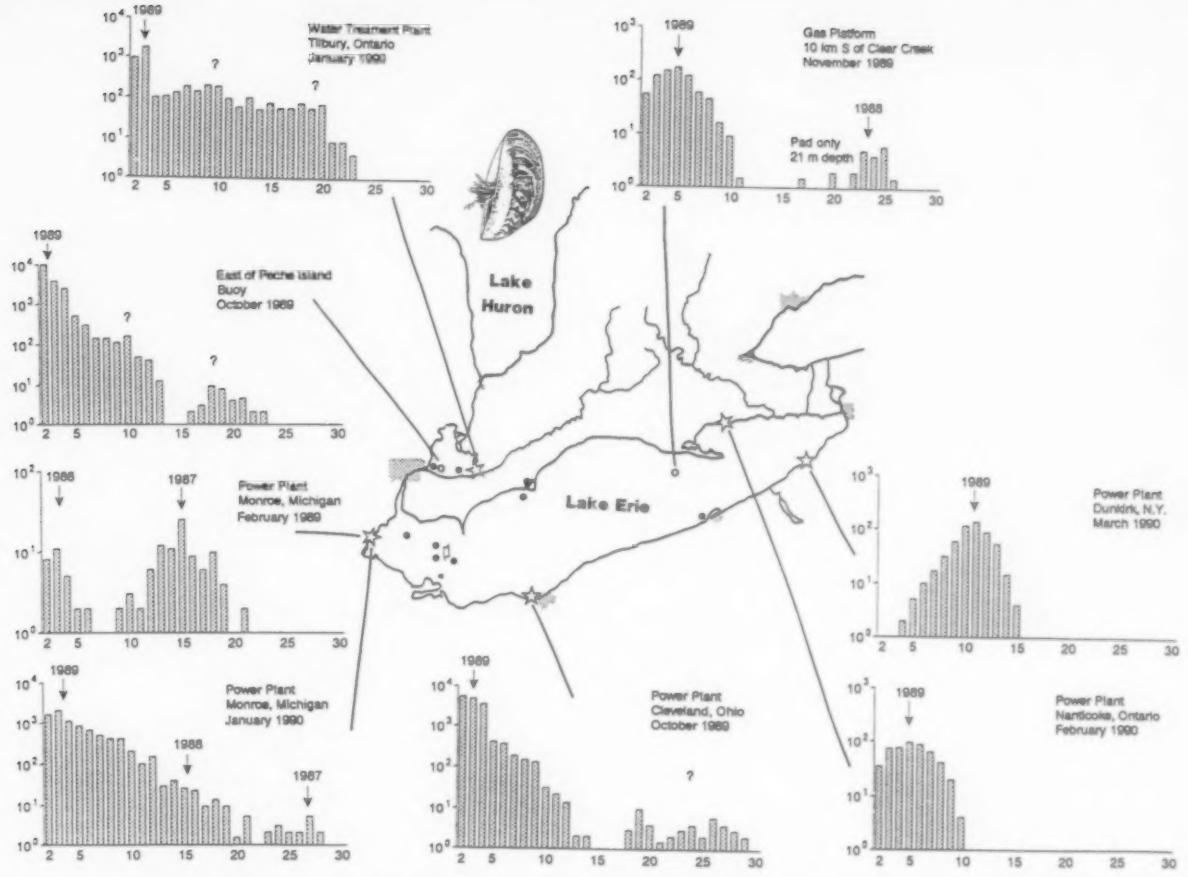


FIG. 3. Length–frequency histograms of *D. polymorpha* from seven industrial and pelagic sites in the Great Lakes. Shell length (mm) is marked on the abscissa and number of animals is represented on the ordinate. Location, sampling depth, and date are noted on each histogram. Arrows indicate modes (= cohorts). Date above arrows indicates the year of settlement for the cohort.

may have been present. A fourth year-class is usually difficult to detect because most individuals never reach the age of 4 (Kornobis 1977; Morton 1969; Wiktor 1963).

Spatial Distribution

The length–frequency analyses suggest that the spatial distribution of *Dreissena* at the end of 1986 was probably restricted to the southwestern corner of Lake St. Clair, the Detroit River, and the central portion of the western basin of Lake Erie (Fig. 4A). We believe that these individuals constituted the founding population for the Great Lakes. Historical benthic invertebrate studies conducted in 1983 and 1984 in the Detroit River, in 1983, 1984, and 1986 in Lake St. Clair, and in 1983, 1984, and 1985 in St. Clair River did not report a single specimen (Hudson et al. 1986; Griffiths 1987, 1989b; Nalepa and Gauvin 1988). Thus, it is unlikely that *Dreissena* had established itself before 1986. Furthermore, the southwestern corner of Lake St. Clair seems the most probable location from which the population expanded. The shallowness of the lake means that the risk to ships of grounding is greater than elsewhere in the St. Lawrence Seaway. If a ship does become beached, releasing ballast water is one method of freeing the vessel. Once *Dreissena* was discharged into the lake, the surface currents then would disperse the veligers throughout the southern area of the lake and into the Detroit River (Edsall et al. 1988) and then into Lake Erie towards Pelee Island (Hamblin 1971).

The length–frequency analyses suggest that the spatial distribution of *Dreissena* at the end of 1987 extended from the southern portion of Lake St. Clair, through the Detroit River, into the western end of Lake Erie and along the north shore of Lake Erie to Rondeau Bay (Fig. 4B). Veligers were not found in the zooplankton community of Rondeau Bay in August of 1987 (R. W. Griffiths, unpubl. data), and juveniles were not observed in the Kelly Island area until 1988 (Haag and Garton 1991), possibly because the surface currents tended to move the veligers in a more north and easterly direction (Hamblin 1971).

The spatial distribution of *Dreissena* at the end of 1988 ranged from the southern half of Lake St. Clair (Hebert et al. 1989) to the central basin of Lake Erie (Griffiths 1989a) (Fig. 4C). The length–frequency analyses suggest that *Dreissena* was not present in the eastern basin of Lake Erie (Fig. 2 and 3), and no mussels were found on Canadian navigational buoys, beaches, or water treatment plants located east of Long Point. Veligers appeared in the western basin in June and in the central basin of Lake Erie in July of 1988 (J. Leach, unpubl. data). *Dreissena* was present at Cleveland, but we have no informa-

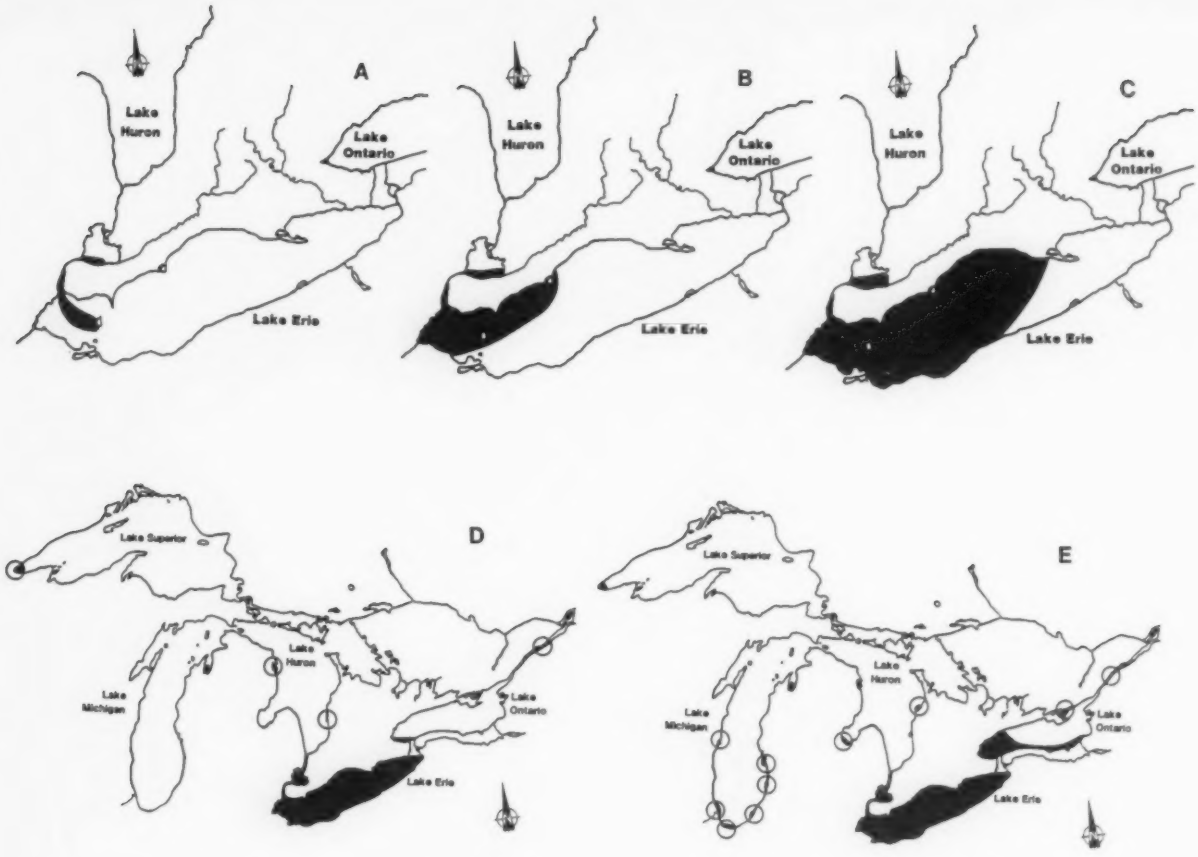


FIG. 4. Estimated distribution of *D. polymorpha* in the Great Lakes basin at the end of (A) 1986, (B) 1987, (C) 1988, (D) 1989, and (E) 1990. Shaded area indicates the zebra mussel range. Open circles indicate establishment of isolated populations.

tion about how far east of Cleveland along the U.S. shoreline of Lake Erie they occurred. Surface currents would have tended to push the free-swimming larvae (i.e. veligers) in an eastward direction along the centre of the lake and not directly towards the U.S. shoreline (Hamblin 1971).

At the end of 1989, zebra mussels were distributed from Marine City, located on the St. Clair River, through Lake St. Clair, the Detroit River, Lake Erie, the Welland Canal, and Niagara River to Pt. Weller and Hamilton Harbour in the western basin of Lake Ontario (Fig. 4D). To briefly summarize their locations, zebra mussels were found at American electrical generating plants located along the southern half of the St. Clair River, the Detroit River, and along the shore of Lake Erie, all Canadian water treatment plants that take water from Lake St. Clair, the Detroit River, the western and central basins of Lake Erie, the Niagara River, and American water treatment plants in Detroit, Monroe, Toledo, Cleveland, Erie, and Buffalo. Infestations of *Dreissena* were found in the pipes of two metal casting foundries, one in Windsor and the other in St. Catherines. In the autumn of 1989, a band of mussel shells up to a 30 cm deep was seen at numerous beaches along the north shore of Lake Erie from west of Pt. Pelee to west of Port Stanley. Individuals and small groups of *Dreissena* were also noted along beaches on Long Point and at Nanticoke, Port Colbourne, and Fort Erie.

In addition, isolated populations were found near Cornwall, Ontario, in the St. Lawrence River, in the harbour at Duluth, Wisconsin, in Lake Superior, and the harbours at Alpena, Michigan, and Goderich, Ontario, in Lake Huron (Fig. 4D). Mussels were also observed on ships and barges in Sturgeon Bay in Lake Michigan (Kraft 1990a).

At the end of 1990, zebra mussels ranged from the head of the St. Clair River to the western basin and southern shoreline of Lake Ontario (Fig. 4E). In Lake Ontario, mussels were found at several sites along the north shore from Hamilton to the Darlington Nuclear Power Station, located east of Oshawa, and along the south shore from the Niagara River to Oswego (Kraft 1990c). They were also observed in the New York State Barge Canal from the Niagara River to east of Rochester (Kraft 1990c). Isolated populations were found at several harbours in Lake Michigan (Kraft 1990b, 1990c, 1991), Saginaw Bay and Pt. Elgin on Lake Huron, at Picton, Bath, and Kingston in the eastern basin of Lake Ontario, and at Prescott on the St. Lawrence River. Mussels were observed on boats in inland lakes of Ohio (Kraft 1991) and along the Kentucky–Tennessee border (J. A. Drake, University of Tennessee at Knoxville, pers. comm.). However, established mussel populations have not

been reported from inland lakes on either side of the Great Lakes.

Dispersal Mechanisms and Routes

The rapid downstream dispersal of *Dreissena* in the lower Great Lakes can be attributed to two biological characteristics: high female fecundity, 10^4–10^6 eggs·yr^{-1} (Walz 1978a), and a pelagic larval stage, a unique feature among freshwater bivalves. In the western basin of Lake Erie, veligers were present in the water from June to October in 1989 at concentrations as high as 200 000·m^{-3} (J. Leach, unpubl. data). These individuals can be carried great distances by surface currents during the 5–16 d (depending on water temperatures) that they remain in the plankton (Kornobis 1977; Stanczykowska 1977; Lewandowski 1982). After settling, juvenile mussels may again enter the drift, using byssal threads as drag lines (bysso-pelagic transport). The passive drift of veligers and juveniles alone probably accounted for the rapid colonization of Lake Erie in just 3 yr, which is about the residence time (2.7 yr) for water in the lake.

The appearance of isolated zebra mussel populations in numerous harbours throughout the Great Lakes suggests that human activities associated with commercial shipping, boating (research and pleasure), and fishing activities also aided the dispersal of the mussel. Millions of tonnes of cargo, primarily coal, limestone, and iron ore, are transported from the upper Great Lakes to ports in Lake Erie every year (Edsall et al. 1988). These ships upon returning to their ports then discharge their ballast water taken from Lake Erie. Commercial ships, therefore, are a likely vector for dispersing zebra mussels to harbours throughout the Great Lakes. Ships carrying freshwater ballast from European ports are a probable additional vector, one that may have been responsible for establishing some of the harbour populations. However, the voluntary regulation imposed on ocean-crossing ships entering the St. Lawrence Seaway in May of 1989 that instructs them to exchange ballast water over the deep ocean should have decreased the probability of additional introductions from Europe.

In addition, small boats that enter zebra mussel infested waters are potential vectors for transporting juvenile mussels throughout the basin, either by water or overland when the craft is trailered, because boat hulls provide good habitat for settling mussels. Individuals were found to survive for 4 d out of water in the interior of a car pulled out of Lake Erie in the summer of 1989 (R. W. Griffiths, unpubl. data). Thus, it is possible that *Dreissena* attached to the hulls of boats may survive overland journeys, since many inland waterways are well within a 4-d trip from the Great Lakes.

Live bait, purchased from shops along Lake Erie and Lake St. Clair, which are maintained in raw lake water are also a potential vector for the transport of veligers to inland waterways. Bait bucket release has been implicated for the spread of other species, such as the threespine stickleback (*Gasterosteus aculeatus*) (Stedman and Bowen 1985) and the crayfish (*Orconectes obscurus*) (Crocker and Barr 1968), into the Great Lakes basin.

The dispersal of *Dreissena* beyond the Great Lakes drainage basin will occur as a result of both passive drift and human activities. Veligers can drift eastward to the Hudson River via the New York State Barge Canal and southward to the Mississippi River via the Chicago Sanitary and Ship Canal and the Illinois River. Fisherman and boaters can easily trailer boats from the lower Great Lakes to numerous inland waterbodies in Ontario and the Great Lakes states within a day's travel. Each autumn, American boats are trailered from Lake Erie to waterbodies in the southeastern United States for the winter via Interstates 77 and 79, thus providing the mussels with long-range dispersal routes to the Mississippi and Atlantic drainage basins.

The downstream dispersal of *Dreissena* from established areas by passive transport can be estimated from current flow information. In contrast, the dispersal of *Dreissena* by human activities is more difficult to predict. The appearance of *Corbicula* in the Ohio River in 1957, when its known range was confined to the western United States (McMahon 1982), illustrates the dispersal leaps that are possible when human activities become a primary vector. Virtually any waterbody that can be reached by boaters and fisherman within a few days' travel of the lower Great Lakes, particularly Lake Erie, is at risk of invasion from this nuisance species.

Acknowledgements

Many people assisted with the collection of data for this study. In particular, we would like to acknowledge the help of Doug Huber and John Westwood of the Ministry of the Environment and Ivan Bottoms and Lee Suton of the Detroit River Yachting Association. Danuta Zaranko and Sonya Gutschi conducted most of the shell measurements. Helpful comments were provided by Ian Davies and an anonymous reviewer.

References

AFANAS'YEV, S. A., AND A. A. PROTASOV. 1987. Characteristics of *Dreissena* populations in the periphyton of nuclear power plant cooling ponds. Hydrobiol. J. 23: 42–49.

ARTER, H. E. 1989. Effect of eutrophication on species composition and growth of freshwater mussels (Mollusca, Unionidae) in Lake Hallwil (Aargau, Switzerland). Aquat. Sci. 51: 87–99.

BARTON, D. R., AND M. GRIFFITHS. 1984. Benthic invertebrates of the nearshore zone of eastern Lake Huron, Georgian Bay and North Channel. J. Great Lakes Res. 10: 407–416.

BERG, K. 1938. Studies of the bottom animals of Esrom Lake. Mem. Acad. R. Sci. Lett. Denmark Ser. 9, 8: 1–255.

BERG, D. J., AND D. W. GARTON. 1988. Seasonal abundance of the exotic predatory cladoceran, *Bythothrephes cederstroemi*, in western Lake Erie. J. Great Lakes Res. 14: 479–488.

BIJ DE VAATE, A. 1991. Distribution and aspects of population dynamics of the zebra mussel, *Dreissena polymorpha* (Pallis, 1771), in the lake IJsselmeer area (the Netherlands). Oecologia 86: 40–50.

CLARKE, K. B. 1952. The infestation of waterworks by *Dreissena polymorpha*, a fresh water mussel. J. Inst. Water Eng. 6: 370–379.

CROCKER, D. W., AND D. W. BARR. 1968. Handbook of the crayfishes of Ontario. University of Toronto Press, Toronto, Ont. 158 p.

EDSALL, T. A., B. A. MANNY, AND C. N. RAPHAEL. 1988. The St. Clair River and Lake St. Clair, Michigan: an ecological profile. U.S. Fish Wildl. Serv. Biol. Rep. 85(7.3): 130 p.

EHRENBERG, H. 1957. Die Steinfauna der Brandungsufer ostholsteinischer Seen. Arch. Hydrobiol. 53: 87–159.

GREENSHIELDS, F., AND J. E. RIDLEY. 1957. Some researches on the control of mussels in water pipes. J. Inst. Water Eng. 11: 300–306.

GRIFFITHS, R. W. 1987. Environmental quality measurement of Lake St. Clair in 1983 as reflected by the distribution of benthic invertebrate communities. Ontario Ministry of the Environment, London, Ont. 35 p.

1989a. Introduction of zebra mussels into the Great Lakes: truth and consequences. Monthly News Letter No. 45. Ontario Ministry of the Environment, London, Ont. 1 p.

1989b. Environmental quality assessment of the St. Clair River as reflected by the 1985 distribution of benthic invertebrates. Prepared for the Ontario Ministry of the Environment, London, Ont. 41 p.

GRIFFITHS, R. W., W. P. KOVALAK, AND D. W. SCHLOESSER. 1989. The zebra mussel, *Dreissena polymorpha* (Pallas, 1771), in North America: impact on raw water users, p. 11–27. *In* Proceedings: EPRI Service Water System Reliability Improvement Seminar. Electric Power Research Institute, Palo Alto, CA.

HAAG, W. R., AND D. W. GARTON. 1991. Synchronous spawning in a recently established population of the European zebra mussel, *Dreissena polymorpha*, in western Lake Erie. Hydrobiologia (In press)

HAMBLIN, P. F. 1971. Circulation and water movement in Lake Erie. Scientific Series No. 7. Inland Waters Branch, Department of Energy, Mines and Resources, Ottawa, Ont. 50 p.

HAMBURGER, K., P. C. DALL, AND P. M. JONASSON. 1990. The role of *Dreissena polymorpha* Pallas (Mollusca) in the energy budget of Lake Esrom, Denmark. Verh. Int. Ver. Limnol. 24: 621–625.

HEBERT, P. D. N., B. W. MUNCASTER, AND G. L. MACKIE. 1989. Ecological and genetic studies on *Dreissena polymorpha* (Pallas): a new mollusc in the Great Lakes. Can. J. Fish. Aquat. Sci. 46: 1587–1591.

HEBERT, P. D. N., C. C. WILSON, M. H. MURDOCH, AND R. LAZAR. 1991. Demography and ecological impacts of the invading mollusc, *Dreissena polymorpha*. Can. J. Zool. 69. (In press)

HUDSON, P. L., B. M. DAVIS, S. J. NICHOLS, AND C. M. TOMCKO. 1986. Environmental Studies of macrozoobenthos, aquatic macrophytes and juvenile fishes in the St. Clair – Detroit River system, 1983–1984. National Fisheries Research Centre - Great Lakes, U.S. Fish and Wildlife Service, Ann Arbor, MI. 116 p.

JENNER, H. A., AND J. P. M. MOMMEN. 1985. Driehoeksmosselen en aangroeiproblemen. H_2O 18: 2–6.

KACHANOVA, A. A. 1962. The ecology of *Dreissena polymorpha* in the Uchinsk reservoir. Vop. Ekol. Vyssh. Shbala, Moscow, 5: 94–95.

KHARCHENKO, T. A., AND A. V. LYASHENKO. 1985. Destruction of allochthonous organic matter in canals in the presence of *Dreissena*. Hydrobiol. J. 21: 93–98.

KORNOBIS, S. 1977. Ecology of *Dreissena polymorpha* (Pall.) (Dreissenidae, Bivalvia) in lakes receiving heated water discharges. Pol. Arch. Hydrobiol. 24: 531–545.

KRAFT, C. 1990a. Zebra mussel update #1. University of Wisconsin Sea Grant Institute, Madison, WI. 3 p.

1990b. Zebra mussel update #4. University of Wisconsin Sea Grant Institute, Madison, WI. 3 p.

1990c. Zebra mussel update #5. University of Wisconsin Sea Grant Institute, Madison, WI. 4 p.

1991. Zebra mussel update #6. University of Wisconsin Sea Grant Institute, Madison, WI. 4 p.

LANE, D. J. W., J. A. NOTT, AND D. J. CRISP. 1982. Enlarged stem gland in the foot of post-larval mussel *Mytilus edulis*: adaptation for byssopelagic migration. J. Mar. Biol. Assoc. U.K. 62: 809–818.

LEWANDOWSKI, K. 1976. Unionidae as a substratum for *Dreissena polymorpha* Pall. Pol. Arch. Hydrobiol. 23: 409–420.

1982. The role of early development stages in the dynamics of *Dreissena polymorpha* (Pall.) (Bivalvia) populations in lakes. II. Settling of larvae and the dynamics of numbers of settled individuals. Ekol. Pol. 30: 223–286.

1983. Formation of annuli on shells of young *Dreissena polymorpha* (Pall.). Pol. Arch. Hydrobiol. 30: 343–351.

LUNDBECK, J. 1926. Die Bodentierwelt Norddeutscher Seen. Arch. Hydrobiol. Suppl. 7: 1–470.

L'VOV, A. A. 1980. Ecology of *Dreissena* (*Dreissena polymorpha* (Poll.)), p. 101–119. *In* Benthos of the Uchinsk Reservoir. Nauka, Moscow.

MCMAHON, R. F. 1982. The occurrence and spread of the introduced Asiatic freshwater clam, *Corbicula fluminea* (Muller), in North America: 1924–1982. The Nautilus 96: 134–141.

MORTON, B. S. 1969. Studies on the biology of *Dreissena polymorpha* Pall. III. Population dynamics. Proc. Malacol. Soc. Lond. 38: 471–482.

1979. Freshwater fouling bivalves. Proceedings, First International *Corbicula* Symposium. Texas Christian University. Fort Worth, Texas, October 13–15, 1977. 14 p.

NALEPA, T. F., AND J. M. GAUVIN. 1988. Distribution, abundance and biomass of freshwater mussels (Bivalvia: Unionidae) in Lake St. Clair. J. Great Lakes Res. 14: 411–419.

PREZANT, R. S., AND K. CHALERMWAT. 1984. Floatation of the bivalve *Corbicula fluminea* as a means of dispersal. Science (Wash., DC) 225: 1491–1493.

SCHLOESSER, D. W., P. L. HUDSON, AND S. J. NICHOLS. 1986. Distribution and habitat of *Nitellopsis obtusa* (Characeae) in the Laurentian Great Lakes. Hydrobiologia 133: 91–96.

SCHORMANN, J., J. T. CARLTON, AND M. R. DOCHODA. 1990. The ship as a vector in biotic invasions. IMAS 90, Marine Technology and the Environment, Paper 19, p. 147–152. Trans. IMar E (C) Vol. 102: Conf. 2. Marine Mgmt. (Holdings) Ltd., London, England. 189 p.

SEBESTYEN, O. 1938. Colonization of two new fauna-elements of Pontus-origin (*Dreissena polymorpha* Pall. and *Corophium curvisinum* (G. O. Sars forma devium Wundsch) in Lake Balaton. Verh. Int. Ver. Limnol. 8: 169–181.

SHEVTSOVA, L. V., AND T. A. KHARCHENKO. 1981. The role of *Dreissena* in reworking suspended organic matter in the North-Crimean Canal. Hydrobiol. J. 17: 33–36.

SHTEGMAN, B. K. [ED.] 1964. Biology and control of *Dreissena*: a collection of papers. Academy of Sciences of the USSR, Institute of Biology and Inland Waters, Leningrad 7: 1–145. (Translated from Russian)

SPRUNG, M. 1987. Ecological requirements of developing *Dreissena polymorpha* eggs. Arch. Hydrobiol. Suppl. 79: 69–86.

STANCZYKOWSKA, A. 1977. Ecology of *Dreissena polymorpha* (Pallas) (Bivalvia) in lakes. Pol. Arch. Hydrobiol. 24: 461–530.

STANCZYKOWSKA, A., W. LAWACZ, J. MATTICE, AND K. LEWANDOWSKI. 1976. Bivalves as a factor effecting circulation of matter in Lake Mikolajskie (Poland). Limnologica (Berlin) 10: 347–352.

STANCZYKOWSKA, A., AND M. PLANTER. 1985. Factors affecting nutrient budget in lakes of the R. Jorka watershed (Masurian Lakeland, Poland). X. Role of the mussel *Dreissena polymorpha* (Pall.) in N and P cycles in a lake ecosystem. Ekol. Pol. 33: 345–356.

STEDMAN, R. M., AND C. A. BOWEN, II. 1985. Introduction and spread of the threespine stickleback (*Gasterosteus aculeatus*) in Lakes Huron and Michigan. J. Great Lakes Res. 11: 508–511.

VON WINKLE, W. JR. 1970. Effect of environmental factors on byssal thread formation. Mar. Biol. 7: 143–148.

WALZ, N. 1973. Studies on the biology of *Dreissena polymorpha* Pallas in the Lake of Constance. Arch. Hydrobiol. Suppl. 42: 452–482.

1978a. The energy balance of the freshwater mussel *Dreissena polymorpha* Pallas in laboratory experiments and in Lake Constance. II. Reproduction. Arch. Hydrobiol. Suppl. 55: 106–119.

1978b. The production and significance of the *Dreissena* population in the nutrient cycle in Lake Constance. Arch. Hydrobiol. 82: 482–499.

WIKTOR, J. 1963. Research on the ecology of *Dreissena polymorpha* Pall. in the Szczecin Lagoon. Ekol. Pol. 11: 275–280.

YOUNG, C. M., AND J. I. CAMPBELL. 1968. On the heteromyarian condition in the Bivalvia with special reference to *Dreissena polymorpha* and certain Mytilacea. Trans. R. Soc. Edinb. 68: 21–43.

Projected Distribution of the Zebra Mussel, *Dreissena polymorpha*, in North America[1]

David L. Strayer

Institute of Ecosystem Studies, The New York Botanical Garden, Box AB, Millbrook, NY 12545, USA

Strayer, D. L. 1991. Projected distribution of the zebra mussel, *Dreissena polymorpha*, in North America. Can. J. Fish. Aquat. Sci. 48: 1389–1395.

An analysis of the European distribution of the zebra mussel, *Dreissena polymorpha*, shows that the species probably will spread over much of North America. Only softwater districts and the extreme northern and southern parts of the continent are unlikely to be colonized. Within this range, *D. polymorpha* is most likely to be found in large, hardwater lakes and in running waters more than 30 m wide. Populations of *D. polymorpha* probably will spread over a larger part of the lake bottom in shallow, warm lakes than in deep, cold lakes. I could not make any predictions about the expected population densities of *D. polymorpha* in either lakes or streams.

Une analyse de la répartition européenne de la moule zébrée, *Dreissena polymorpha*, indique que cette espèce s'étendra probablement sur la plus grande partie de l'Amérique du Nord. Seules les zones d'eau douce des extrémités nord et sud du continent ne seront vraisemblablement pas colonisées. Dans ce territoire, on trouvera vraisemblablement *D. polymorpha* dans les gros lacs d'eau calcaire, ainsi que dans les cours d'eau de plus de 30 m de largeur. Les populations de *D. polymorpha* couvriront probablement une plus grande partie des fonds des lacs chauds et peu profonds, plutôt que ceux des lacs froids et profonds. Je ne peux faire aucune prévision concernant les densités de population prévues de *D. polymorpha* dans les lacs ou les cours d'eau.

Received August 15, 1990
Accepted April 9, 1991
(JA687)

Reçu le 15 août 1990
Accepté le 9 avril 1991

The zebra mussel, *Dreissena polymorpha* Pallas, was introduced into North America in 1985 and already is spreading widely through the lower Great Lakes (Hebert et al. 1989; Mackie et al. 1989). As the ecological and economic impacts of populations of *D. polymorpha* can be very great (e.g. Stańczykowska 1977; Mackie et al. 1989), it is of considerable interest to know how far the species will spread in North America and how abundant it will become in various parts of this new range. McMahon and Tsou (1990) already have made a preliminary assessment of the possible range of *D. polymorpha* in North America based on its thermal biology, but did not address other potentially limiting factors or the question of abundance. The purpose of this paper is to use information on the distribution and abundance of *D. polymorpha* in Europe, where it has long been established, to try to predict its eventual distribution and abundance in North America.

My approach was to analyze data on the European distribution of *D. polymorpha* in the hopes of finding environmental variables that can be used to predict the range limits or abundance of this species in North America. I chose environmental predictor variables that have been suggested to affect *D. polymorpha* and that were readily available from published sources. Factors that have been suggested to limit growth or distribution of *D. polymorpha* include low or high temperature, low calcium concentrations, and very high or very low lake productivity.

Although low temperature is unlikely to kill *D. polymorpha* outright, it may limit the growing season for this species; Morton (1969) suggested that growth of *D. polymorpha* does not occur at water temperatures below approximately 10°C. In addition, larvae are released and develop only in warm waters (Stańczykowska 1977; Lewandowski 1982a; Sprung 1987). *Dreissena polymorpha* may, therefore, be kept out of cool waters because the period available for growth and reproduction is too short. Walz (1978) showed that respiratory costs can exceed assimilation rates of *D. polymorpha* at high temperatures (at least in large adult specimens), resulting in long periods of negative growth which may prevent *D. polymorpha* from living in very warm waters. In addition, very warm waters (>26–32°C) may kill larvae or adults of *D. polymorpha* outright (McMahon and Tsou 1990). Developing eggs of *D. polymorpha* may require high calcium concentrations (approximately 1 meq/L) (Sprung 1987), so the species may be restricted to hard waters.

Stańczykowska et al. (1983) found that *D. polymorpha* was found infrequently in hypereutrophic Polish lakes, although they did not offer an explanation for this pattern. It is possible that *D. polymorpha* populations in very productive lakes may be killed during periods of winter anoxia, or even by summer anoxia during periods of still weather (cf. Britt 1955). At the other extreme, the plankton of very unproductive lakes might be too poor to satisfy the dietary requirements of *D. polymorpha* (cf. Walz 1978).

The following analysis contains two parts: an attempt to predict the ultimate range of *D. polymorpha* in North America and an attempt to predict the distribution and abundance of *D. polymorpha* in lakes and streams within that range.

Methods

For the analysis of the range limits of *D. polymorpha* in Europe, I plotted the European distribution of the species

[1]Contribution to the program of the Institute of Ecosystem Studies of The New York Botanical Garden.

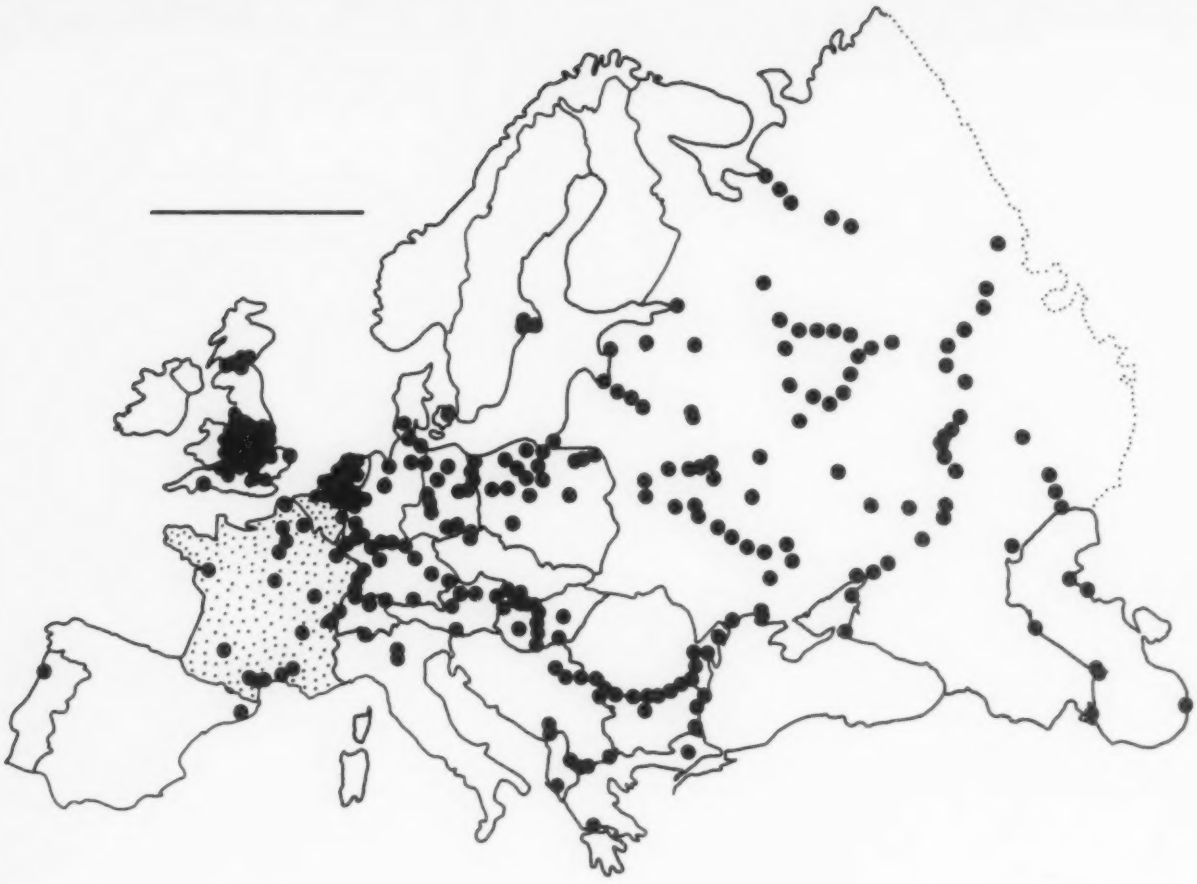


FIG. 1. Records of the occurrence of *D. polymorpha* in Europe (black circles). The species is generally distributed in stippled areas (see text). The record from Oporto, Portugal, sometimes is regarded as spurious (e.g. Willmann and Pieper 1978). Scale bar = 1000 km.

TABLE 1. Range of environmental conditions for weather stations inside and outside the range of *D. polymorpha* in Europe. "Regularity of precipitation" is the ratio of the lowest monthly mean precipitation to the highest monthly mean precipitation.

	Inside	Outside
Mean annual temperature (°C)	−0.6 to 17.6	0.1 to 18.9
Highest monthly mean temperature (°C)	13.3 to 26.4	12.8 to 28.0
Lowest monthly mean temperature (°C)	−15.4 to 9.7	−15.2 to 12.5
Number of warm months	3 to 11	2 to 12
Mean annual precipitation (mm)	130 to 1742	362 to 2504
Regularity of precipitation	0.01 to 0.71	0.01 to 0.60

(Fig. 1), using records from 44 works on the distribution of *D. polymorpha* and other freshwater mollusks in Europe.[2] The stippled areas shown in Fig. 1 were defined as within *D. polymorpha*'s range on the basis of statements that *D. polymorpha* is "common or very common in all of France" (Germain 1931) and "very common in the rivers and canals of middle and lower Belgium" (Adam 1960), despite the paucity of specific locality records from these areas. Then, I selected 110 weather stations from those listed by Wallén (1970, 1977) and Lydolph (1977) and recorded data on mean annual air temperature, highest monthly mean air temperature, lowest monthly mean air temperature, number of months having a mean air temperature ≥10°C ("warm months"), length of the frost-free season (this parameter was available for only 68 of the weather stations), mean annual precipitation, and regularity of precipitation (ratio of lowest to highest monthly mean precipitation). I considered a weather station to lie within the range of *D. polymorpha* if any of the records plotted in Fig. 1 fell within 100 km of the station.

[2]A listing of these sources and all the primary data used in this paper are available at a nominal cost from the author or from the Depository of Unpublished Data, CISTI, National Research Council of Canada, Ottawa, Ont. K1A 0S2, Canada.

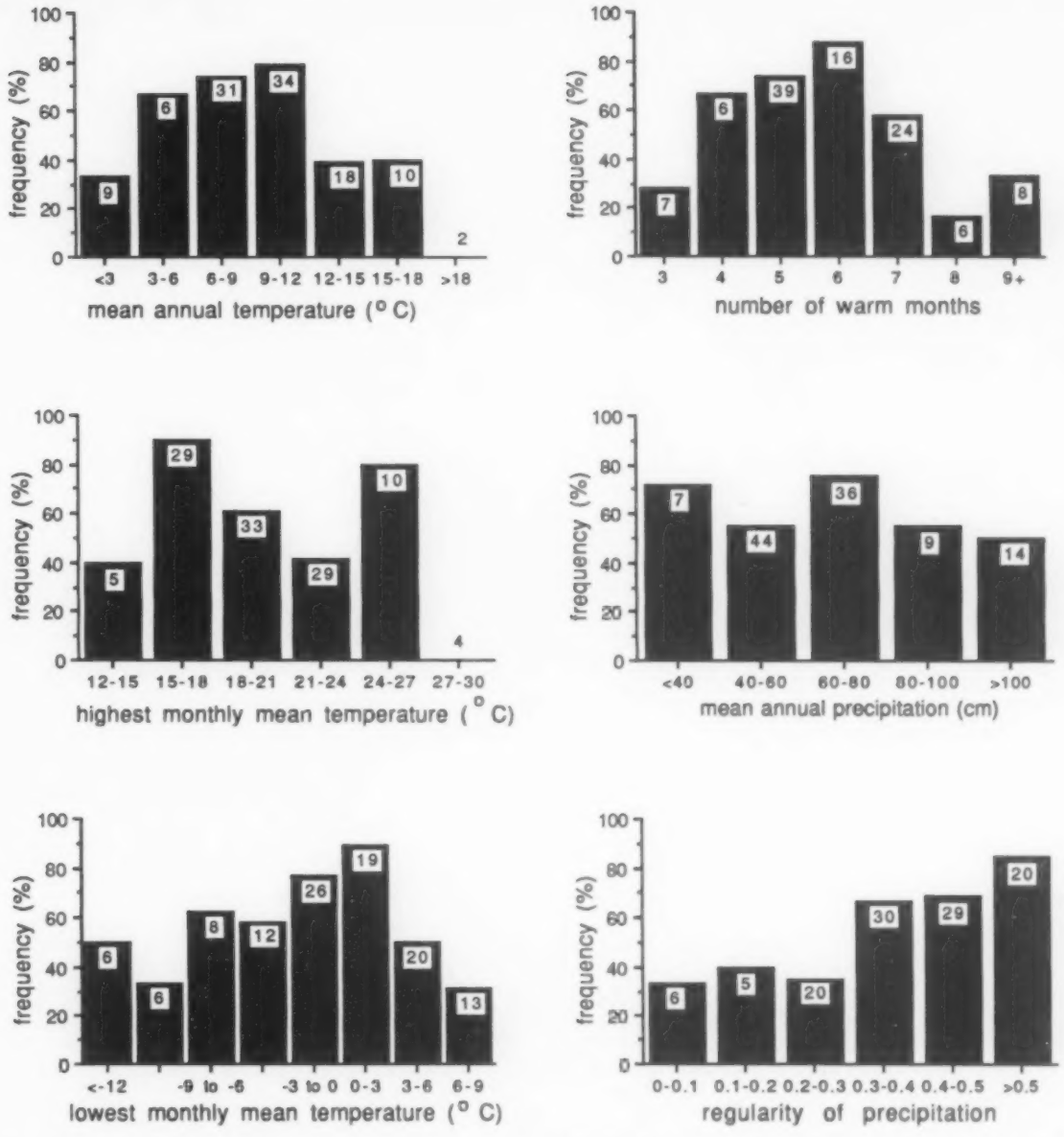


FIG. 2. Frequency of occurrence of *D. polymorpha* near European weather stations as a function of various climatic variables. Numbers in bars show the number of weather stations in each interval.

To predict the abundance of *D. polymorpha* in lakes, I gathered data on the density and bathymetric extent of populations of *D. polymorpha*, along with the values of several environmental parameters, in 70 lakes within the European range of the species. Data collected included the bathymetric zone occupied by *D. polymorpha* (expressed as a percentage of the lake area), the mean population density of *D. polymorpha* within this bathymetric zone ("local density"), the mean population density of *D. polymorpha* over the entire lake ("lakewide density"), the surface area of the lake, the mean depth of the lake, the "hardness" (see below) of the lake water, the Secchi disk transparency, and the mean annual air temperature at a weather station near the lake. Not all of these data were available for all 70 lakes. Although it would be desirable to weight densities of *D. polymorpha* by the areas of various depth strata in a lake, appropriate morphometric data or maps were not available for all lakes. Consequently, the data set contains a mixture of weighted and unweighted means. Because neither calcium concentration nor alkalinity was available for all lakes, I used as an index of water hardness either the calcium concentration or the alkalinity (both expressed as milliequivalents per litre). If both parameters were reported for a lake, I used the mean of the two measurements.

FIG. 3. Approximate potential range limits for *D. polymorpha* in North America, based on the range of temperatures tolerated in Europe. The solid lines show mean annual air temperatures of 0 and 18°C; the dotted lines show lowest monthly mean air temperature of −15°C and highest monthly mean air temperature of 27°C. Climatic data from United States Department of Commerce (1965), Hammond, Inc. (1966), United States Environmental Data Service (1975), and van der Leeden et al. (1990).

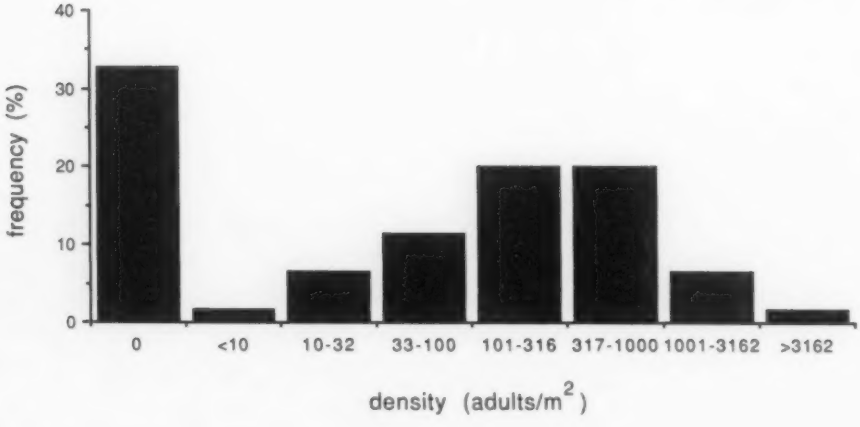


FIG. 4. Lakewide densities of adult *D. polymorpha* in lakes (n = 57) within its European range.

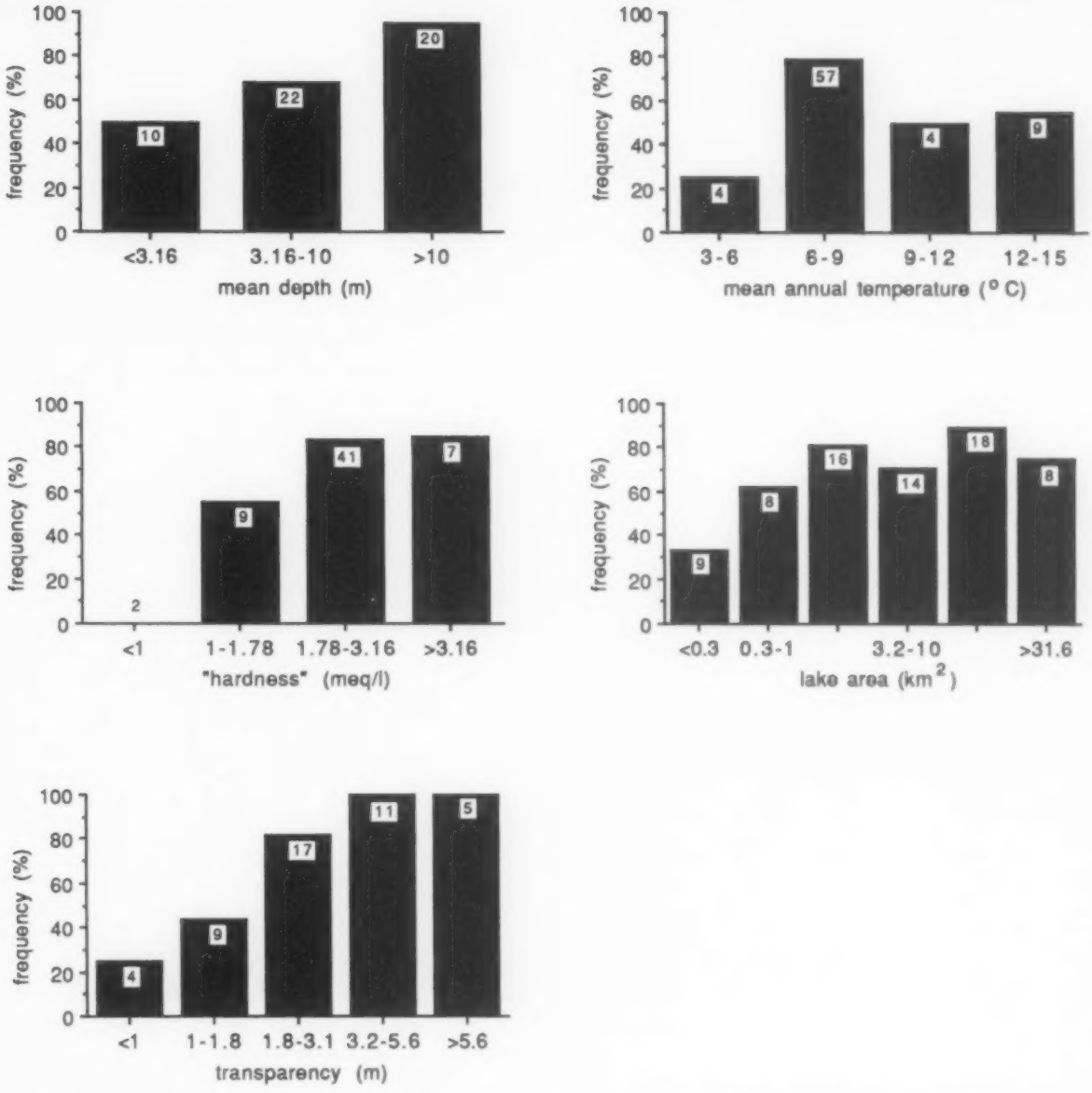


FIG. 5. Frequency of occurrence of *D. polymorpha* in European lakes as a function of various limnological and climatic variables. Numbers in bars show the number of lakes in each interval.

Statistical analyses included simple and stepwise multiple regressions (maximum r^2 method) and simple discriminant analyses using SAS (SAS Institute Inc. 1987) and Ludwig and Reynolds (1988).

Results and Discussion

Range Limits of *D. polymorpha*

Dreissena polymorpha occurs under most climatological conditions found in Europe, in terms of the parameters included in my analysis (Table 1). It is found less frequently in areas of very warm temperature or strongly seasonal precipitation than elsewhere (Fig. 2). A simple discriminant analysis likewise indicates that highest monthly mean temperature and regularity of precipitation differ weakly among sites with and without *D. polymorpha* ($F = 3.28$, $p < 0.01$, accounting for 16% of the variation among sites). The absence of the species from most of the Iberian Peninsula, Italy, and Scandinavia may be because it has not yet dispersed into most waters in these regions, and in the case of Scandinavia because many of the surface waters are too soft to support *D. polymorpha* (see below). *Dreissena polymorpha* has crossed the Alps and

TABLE 2. Frequency of occurrence of *D. polymorpha* in European streams of various widths. Data compiled from 16 European studies.

Width (m)	Frequency (%)	*n*
<3	0	102
3.1 to 10	0	59
10.1 to 30	10	10
30.1 to 100	33	6
>100	83	23

Pyrenees within the last 20 yr or so (Stańczykowska 1977: Margalef 1983).

Because the European range limits of *D. polymorpha* thus probably are not set by climate, it is difficult to project the precise North American range limits for this species. Assuming that *D. polymorpha* will be able to tolerate at least as wide a range of climatic conditions in North America as it does in Europe, it is, however, possible to use the climatic ranges spanned in Europe as a minimum estimate of the potential range of *D. polymorpha* in North America. Based on either mean annual temperature or extreme monthly mean temperatures, *D. polymorpha* might be expected to occur over at least most of the continental United States and southern Canada (Fig. 3). McMahon and Tsou (1990) reached a similar conclusion based on their analysis of the thermal biology of *D. polymorpha*.

Water hardness may also limit the distribution of *D. polymorpha* in North America. Except in Scandinavia, most European surface waters are hard (i.e. > 1 meq Ca^{2+}/L). In contrast, many North American waters are very soft. Many species of freshwater mollusks are restricted to fairly hard waters (e.g. Boycott 1936; Økland 1983), and laboratory studies (Sprung 1987) suggest that larvae of *D. polymorpha* may have an extremely high requirement for calcium (approximately 1 meq/L). Although we do not know precisely how much calcium is required for survival and reproduction of *D. polymorpha* in nature, it is reasonable to expect that the waters in many parts of North America will be too soft for *D. polymorpha* to succeed.

The North American range of *D. polymorpha* is therefore likely to encompass most of the lower 48 United States and southern Canada, excluding calcium-poor regions such as the Canadian Shield, New England, the Adirondacks, and much of the Pacific Northwest. Without more precise information on the thermal tolerances of *D. polymorpha*, it is difficult to predict whether the species will be able to survive in regions beyond the thermal limits shown in Fig. 3. It is imprudent to conclude that areas beyond the thermal limits of Fig. 3 will remain free of *D. polymorpha*; in fact, it seems likely that the species will penetrate some distance beyond these limits, at least in thermally equable sites.

Distribution and Abundance of *D. polymorpha* in Lakes

Dreissena polymorpha is not equally abundant (or even present) in all lakes within its European range (Fig. 4). Is it possible to predict accurately the abundance of *D. polymorpha* in a particular lake? I have broken down this problem into three parts: (i) in what lakes is *D. polymorpha* most likely to be present?, (ii) what bathymetric zone of the lake bottom will the population of *D. polymorpha* occupy?, and (iii) how dense will the population be?

Dreissena polymorpha is most often found in fairly large (>30 ha), deep ($\bar{z}$ > 3 m), hardwater (>1–2 meq/L), clear (transparency >2 m) lakes (Fig. 5). A simple discriminant analysis supports this distinction, accounting for 52% of the variation ($F = 14.67, p < 0.01$) among lakes with and without *D. polymorpha*, chiefly on the basis of depth and hardness. This analysis, however, is based on a very small data set: 24 lakes with *D. polymorpha* and only 6 lakes without *D. polymorpha*. The species may be absent from shallow, productive lakes because of the tendency of such lakes to winterkill or because predation from waterbirds in shallow lakes is sufficiently intense to affect populations of *D. polymorpha* (e.g. Suter 1982).

The bathymetric zone occupied by *D. polymorpha* is weakly related (adjusted $r^2 = 0.42, p < 0.01$) to the logarithm of mean depth of the lake and mean annual air temperature and is greatest in shallow, warm lakes. *Dreissena polymorpha* rarely is found on profundal sediments, but instead is typically found in the littoral and sublittoral zones (Stańczykowska 1977). Lakes with shallow mean depths tend to have large littoral and sublittoral zones, and lakes in warm regions tend to have deeper epilimnions than lakes in cold regions (Straškraba 1980).

There were almost no significant correlations between density of *D. polymorpha* and any environmental parameter, alone or in combination. The only statistically significant correlation I found (between local density and mean air temperature) had an r^2 of 0.11. The lack of success in predicting the density of *D. polymorpha* populations from simple environmental variables (Šapkarev 1969; Stańczykowska 1977; this study) probably is due to the small size of the available data sets and the large interannual fluctuations in population density of *D. polymorpha*. Most of the data available for analysis are based on single estimates of population density. Populations of *D. polymorpha* can undergo very wide (approximately three orders of magnitude) swings in density among years (e.g. Stańczykowska 1977, 1978; Lewandowski 1982b), so a single year's estimate is likely to give a very poor estimate of the long-term mean in population density.

Distribution of *D. polymorpha* in Running Waters

Dreissena polymorpha is common and widely distributed in running waters as well as standing waters in Europe. Unfortunately, there are very few quantitative studies on the abundance of *D. polymorpha* in running waters in Europe, and even fewer studies that include quantitative information on environmental factors (e.g. mean discharge, hydrologic variability, local gradient, water chemistry) that could serve as predictor variables. Nonetheless, stream size is clearly related to the presence or absence of the species in Europe (Table 2). *Dreissena polymorpha* occurs frequently in streams more than 30 m wide, but rarely in streams smaller than this. The ecological mechanisms that may restrict *D. polymorpha* to large streams are not known.

Conclusions

Dreissena polymorpha probably will have a wide range in North American rivers and lakes. Within the range shown in Fig. 3, the species probably will ultimately occupy all of the large, hardwater streams. Hardwater lakes likewise will be widely colonized, although small, shallow, highly productive lakes are least likely to support *D. polymorpha*. Several important gaps in knowledge keep us from making precise predictions about the distribution and abundance of *D. polymorpha* in North America. Extreme temperatures and low dissolved calcium

probably will determine the range boundaries of *D. polymorpha* in North America, yet we have only a few laboratory studies on the influence of these environmental factors on *D. polymorpha*. Finally, it is unfortunately not possible on the basis of available data to predict the density of populations of *D. polymorpha* from environmental data.

Acknowledgements

My best thanks go to our librarians Annette Frank and JoAnn Bianchi for their tenacity in locating the papers upon which this analysis was based, to the editor, two thorough referees, and Jon Cole for their comments on the manuscript, and to Robert McMahon for supplying preprints of his work. This work was supported by the Mary Flagler Cary Charitable Trust and the Hudson River Foundation.

References

ADAM, W. 1960. Mollusques. Tome I. Mollusques terrestres et dulcicoles. Faune de Belgique. Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium.

BOYCOTT, A. E. 1936. The habitats of the fresh-water molluscs in Britain. J. Anim. Ecol. 5: 116–186.

BRITT, N. W. 1955. Stratification in western Lake Erie in summer of 1953: effects on the *Hexagenia* (Ephemeroptera) population. Ecology 36: 239–244.

GERMAIN, L. 1931. Mollusques terrestres et fluviatiles, deuxième partie. Faune de France. Vol. 22. Paul Lechevalier, Paris.

HAMMOND, INC. 1966. Hammond Ambassador world atlas. Hammond, Inc., Maplewood, NJ. 352 p.

HEBERT, P. D. N., B. W. MUNCASTER, AND G. L. MACKIE. 1989. Ecological and genetic studies on *Dreissena polymorpha* (Pallas): a new mollusc in the Great Lakes. Can. J. Fish. Aquat. Sci. 46: 1587–1591.

LEWANDOWSKI, K. 1982a. The role of early developmental stages in the dynamics of *Dreissena polymorpha* (Pall.) populations in lakes. I. Occurrence of larvae in the plankton. Ekol. Pol. 30: 81–109.

1982b. O zmiennej liczebności malza (*Dreissena polymorpha* (Pall.). Wiad. Ekol. 28: 141–154.

LUDWIG, J. A., AND J. F. REYNOLDS. 1988. Statistical ecology. Wiley-Interscience, New York, NY. 337 p. + diskette.

LYDOLPH, P. E. 1977. Climates of the Soviet Union. World survey of climatology. Vol. 7. Elsevier Scientific Publishing Company, Amsterdam, The Netherlands.

MACKIE, G. L., W. N. GIBBONS, B. W. MUNCASTER, AND I. M. GRAY. 1989. The zebra mussel, *Dreissena polymorpha*: a synthesis of European experiences and a preview for North America. Environment Ontario. 76 p. + unpaginated appendices.

MARGALEF, R. 1983. Limnologia. Omega, Barcelona. 1010 p.

MCMAHON, R. F., AND J. L. TSOU. 1990. Impact of European zebra mussel infestation to the electric power industry. Proc. Am. Power Conf. 52: 988–997.

MORTON, B. S. 1969. Studies on the biology of *Dreissena polymorpha* Pall. III. Population dynamics. Proc. Malacol. Soc. Lond. 38: 471–482.

ØKLAND, J. 1983. Factors regulating the distribution of freshwater snails (Gastropoda) in Norway. Malacologia 24: 277–288.

ŠAPKAREV, J. A. 1969. Distribution and the population density of *Dreissena polymorpha* Pall. (Lamellibranchia) in the lakes of Macedonia. Annu. Univ. Skopje Fac. Sci. Nat. 21: 31–52. (In Macedonian, with English summary)

SAS INSTITUTE INC. 1987. SAS/STAT guide for personal computers, Version 6 edition. SAS Institute Inc., Cary, NC. 1028 p.

SPRUNG, M. 1987. Ecological requirements of developing *Dreissena polymorpha* eggs. Arch. Hydrobiol. Suppl. 79: 69–86.

STAŃCZYKOWSKA, A. 1977. Ecology of *Dreissena polymorpha* (Pallas) (Bivalvia) in lakes. Pol. Arch. Hydrobiol. 24: 461–530.

1978. Occurrence and dynamics of *Dreissena polymorpha* (Pall.) (Bivalvia). Int. Ver. Theor. Angew. Limnol. Verh. 20: 2431–2434.

STAŃCZYKOWSKA, A., E. JURKIEWICZ-KARNOWSKA, AND K. LEWANDOWSKI. 1983. Ecological characteristics of lakes in north-eastern Poland versus their trophic gradient. X. Occurrence of molluscs in 42 lakes. Ekol. Pol. 31: 459–475.

STRAŠKRABA, M. 1980. The effects of physical variables on freshwater production: analyses based on models, p. 13–84. *In* E. D. LeCren and R. H. Lowe-McConnell [ed.] The functioning of freshwater ecosystems. Cambridge University Press, Cambridge.

SUTER, W. 1982. Der Einfluss von Wasservögeln auf Populationen der Wandermuschel (*Dreissena polymorpha* Pall.) am Untersee/Hochrhein (Bodensee). Schweiz. Z. Hydrol. 44: 149–161.

UNITED STATES DEPARTMENT OF COMMERCE. 1965. World weather records, 1951–60. Vol. 1. North America. Washington, DC. 535 p.

UNITED STATES ENVIRONMENTAL DATA SERVICE. 1975. Weather atlas of the United States. Gale Research Co., Detroit, MI. 262 p.

VAN DER LEEDEN, F., F. L. TROISE, AND D. K. TODD. 1990. The water encyclopedia. 2nd ed. Lewis Publishers, Chelsea, MI. 808 p.

WALLÉN, C. C. [ED.] 1970. Climates of northern and western Europe. World survey of climatology. Vol. 5. Elsevier Scientific Publishing Company, Amsterdam, The Netherlands.

1977. Climates of central and southern Europe. World survey of climatology. Vol. 6. Elsevier Scientific Publishing Company, Amsterdam, The Netherlands.

WALZ, N. 1978. The energy balance of the freshwater mussel *Dreissena polymorpha* in the laboratory and in Lake Constance, Switzerland. Part 3. Growth under standard conditions. Arch. Hydrobiol. Suppl. 55: 121–141.

WILLMANN, R., AND H. PIEPER. 1978. Lamellibranchiata, p. 135–137. *In* J. Illies [ed.] Limnofauna Europaea. 2nd ed. Gustav Fisher Verlag, Stuttgart.

Need for Replicated Electrophoretic Analyses in Multiagency Genetic Stock Identification (GSI) Programs: Examples from a Pink Salmon (*Oncorhynchus gorbuscha*) GSI Fisheries Study

Bruce A. White

Pacific Salmon Commission, 600-1155 Robson Street, Vancouver, B.C. V6E 1B5, Canada

and James B. Shaklee

Washington Department of Fisheries, 115 General Administration Building, Olympia, WA 98504, USA

White, B. A., and J. B. Shaklee. 1991. Need for replicated electrophoretic analyses in multiagency genetic stock identification (GSI) programs: examples from a pink salmon (*Oncorhynchus gorbuscha*) GSI fisheries study. Can. J. Fish. Aquat. Sci. 48: 1396–1407.

Genetic stock identification (GSI) studies usually assume that electrophoretic data from different laboratories are accurate, precise, and comparable. We compared the genetic scores from replicate (identical) collections of pink salmon (*Oncorhynchus gorbuscha*) tissues that were analyzed in a "blind" manner by three different laboratories; scores at 15 genetic systems (18 loci) were compared for 1248 fish. The scores from laboratories A and B consistently agreed. Their average discrepancy rate across all loci was 0.21%, which was approximately 18 times lower than the discrepancy rate of laboratory C (3.86%). Laboratory C also reported data with higher numbers of discrepancies ($P < 0.01$) in their scores of variant genotypes (non-**100/100*) than the other two laboratories. Stock composition estimates using maximum likelihood analysis of the data from laboratories A and B differed by approximately 1% by stock group, while those of laboratory C differed by an average of 8% by stock group from the estimates of the other two laboratories. Our findings demonstrate that different laboratories can, but do not always, produce results that are consistent. Because many GSI programs in North America rely on data contributed by several laboratories, we recommend that testing of replicate samples be incorporated into all multiagency GSI studies.

Des études d'identification du stock génétique (ISG) supposent habituellement que les données d'électrophorèse de différents laboratoires sont exactes, précises et comparables. Nous avons comparé les profils génétiques de collections d'échantillons identiques de tissus de saumon rose (*Oncorhynchus gorbuscha*), qui ont été analysés lors d'un essai en aveugle effectué par trois différents laboratoires; les profils génétiques de 15 systèmes (18 locus) ont été comparés pour 1 248 poissons. Les profils des laboratoires A et B s'accordaient régulièrement. Leur taux moyen de différence pour tous les locus était de 0,21 %, ce qui était environ 18 fois moins que le taux de différence obtenu avec le laboratoire C (3,86 %). Le laboratoire C a également produit des données comportant un nombre plus élevé de différences ($P < 0,01$) dans le profil des génotypes variants (non **100/100*) par rapport aux deux autres laboratoires. Les évaluations de la composition du stock en utilisant l'analyse des ressemblances maximum des données des laboratoires A et B différaient d'environ 1 % par groupe de stock, alors que ceux du laboratoire C différaient par une valeur moyenne de 8 % par groupe de stock, par rapport aux évaluations des deux autres laboratoires. Nos analyses démontrent que des laboratoires différents peuvent produire des résultats reproductibles, mais que ce n'est pas toujours le cas. Parce qu'un grand nombre de programmes d'ISG de l'Amérique du Nord sont basés sur les données fournies par plusieurs laboratoires, nous recommandons que des essais en plusieurs exemplaires des analyses d'électrophorèse soient incorporés dans toutes les études d'ISG faisant appel à plusieurs organismes.

Received August 10, 1990
Accepted February 20, 1991
(JA677)

Reçu le 10 août 1990
Accepté le 20 février 1991

The electrophoretic analysis of allelic isozyme variation has been recognized for many years as a powerful approach for identifying and characterizing different populations of organisms. The technique has been successfully applied to the study of population structure in numerous species of marine and freshwater fishes (Shaklee 1983; Whitmore 1990). Electrophoresis has proven to be especially useful for distinguishing among different stocks of salmonids (Ryman et al. 1979; Loudenslager and Gall 1980; Altukhov 1981; Stahl 1981; Okazaki 1982; Beacham et al. 1985b; Leary et al. 1987; Gharrett et al. 1987; Utter et al. 1989; Bartley and Gall 1990). The combined use of this laboratory methodology for analyzing tissue samples from both spawning (baseline) populations and from unknown mixtures of stocks in fisheries, along with computerized maximum likelihood estimation (MLE) algorithms to estimate stock proportions in mixed-stock fisheries, is often called "genetic stock identification" (GSI).

GSI has been adopted by many agencies for estimating stock contributions to mixed-stock salmon fisheries in North America (e.g. Beacham et al. 1985a; Pella and Milner 1987; Utter et al.

1987; Shaklee et al. 1990b, 1990c). Most early GSI studies of Pacific salmon (*Oncorhynchus* spp.) were small, individual research projects of short duration and therefore required little coordination and standardization of procedures among laboratories. In contrast, nearly all current salmon GSI programs in North America are large and complex in terms of geographic coverage, frequency and magnitude of field sampling, involvement of multiple agencies and laboratories, and management applications.

The increasing multiagency nature of GSI programs along with the growing complexity of electrophoretic analyses inherent in current GSI applications poses formidable challenges to practitioners of the technique. A brief examination of some of the major problems facing GSI programs is warranted because the present study was inspired by concerns that a multilaboratory GSI program was obtaining inconsistent stock composition estimates.

Complications Facing GSI Programs

The application of GSI to the analysis of mixed-stock fisheries of Pacific salmon can be compromised by several factors, including (1) low levels of polymorphism within a species and/or limited genetic differences among stocks, (2) an incomplete or erroneous baseline, (3) inadequate or unrepresentative samples from mixed-stock fisheries, (4) biases in the statistical procedures used to analyze the electrophoretic data, and (5) inaccurate laboratory analyses. Without adequate genetic differences among stocks, GSI is not practical. Even with adequate levels of genetic variation and stock differentiation, it is necessary to develop an accurate and comprehensive baseline. Field sampling personnel are often faced with logistic problems in the collection of baseline samples from a wide geographic area. In many cases, the area of interest spans the jurisdiction of multiple agencies. Additionally, the large numbers of fish that must be analyzed genetically to characterize all spawning stocks appropriate to the baseline often exceed both the sampling capability of single agencies and the processing capacity of individual laboratories. Consequently, many GSI programs require the involvement of several agencies and laboratories to establish adequate baseline databases.

Obtaining representative and adequate numbers of tissue samples from commercial salmon fishery catches constitutes a third complicating factor. Pacific salmon are highly migratory and the majority of fish are harvested in mixed-stock fisheries. Because fish from local stocks are often harvested in distant fisheries, interagency cooperation is frequently needed to sample all of the fisheries of interest, both to provide estimates of stock contributions to each fishery and to determine overall harvest rates for stocks intercepted in multiple fisheries. Additionally, difficulties may be encountered in sampling adequate numbers of salmon that are representative of the overall catches from a fishery (e.g. Kutkuhn 1963; Tomlinson 1971; Steer et al. 1986). Common problems that arise during sampling are the selectivity of certain types of fishing gear for specific stocks of salmon and the fact that many potential sources of fishery samples (e.g. fishing vessels, "buyer" or "packer" boats, and processing plants) often contain mixed catches from several catch areas or even from different fisheries. These factors increase the difficulty of obtaining a representative sample from a particular fishery.

GSI programs can also be confounded by biases resulting from the statistical algorithms that are used to analyze the genetic data. For example, Wood et al. (1987) found that the MLE models that use electrophoretic data in the computation of stock contribution estimates may yield biased estimates under certain conditions. The MLE models have a tendency to overestimate stocks that are minor contributors to fisheries and underestimate stocks that are major contributors.

A fifth complicating factor concerns the collection of electrophoretic data in the laboratory. The success of GSI programs is contingent upon electrophoretic analyses that are accurate and consistent among laboratories. However, electrophoretic protocols vary from laboratory to laboratory and can potentially have a major impact on the comparability of genetic data (Shaklee and Phelps 1990). Procedures such as the particular electrophoretic buffers used, specific experimental conditions (power supply settings, temperature, duration of the run, etc.), and the expertise of the individuals interpreting the isozyme patterns may potentially affect the accuracy and consistency of the results. Previous studies that compared the results of replicated electrophoretic and isoelectric identification of fish species among several laboratories showed important between-laboratory differences (Learson 1969, 1970; Lundstrom 1980, 1983).

Long-term cooperation among agencies will be required to overcome many of the complications to large-scale GSI programs discussed above. To confirm the reliability of electrophoretic data, contributing laboratories should be tested regularly. The present study was undertaken to examine the consistency of electrophoretic data obtained by three laboratories during the in-season analysis of numerous pink salmon (*Oncorhynchus gorbuscha*) fisheries in 1989.

Consistency of Laboratory Analyses Examined in a GSI Program

The Pacific Salmon Treaty (Annex IV, Chapter 4) requires the component of Fraser River pink salmon in fishery catches to be estimated and accounted for wherever these fish are harvested (Pacific Salmon Commission (PSC) 1989). The PSC uses GSI to achieve this goal because other commonly used methods of stock identification such as marking, tagging, morphometrics, and meristics appear to have limited or negligible value for pink salmon to date (Beacham et al. 1988). The Commission's GSI program was initiated in 1985 after Beacham et al. (1985a) reported that there were sufficient differences in the allelic frequencies of 14 loci resolvable in muscle tissue among Fraser River, Puget Sound, and Canadian non-Fraser odd-year pink salmon stocks to provide reasonably accurate stock composition estimates.

Commission researchers noted during preliminary testing of the technique in 1985 and 1987 that although many of the GSI estimates seemed reasonable, a disturbing number of them seemed improbable based on historic observations of the run timing and abundance of specific stocks that were identified in the fishery mixtures. Following these findings, the Commission's GSI program was examined in light of the typical complications discussed above to ascertain the reasons for these improbable results.

We concluded that many of the problems with past GSI estimates could have resulted from inaccurate genetic data collected during electrophoretic analyses of baseline and in-season fishery collections. Two lines of evidence supported this assessment. First, we noted that several baseline stocks sampled in 1983, 1985, and 1987 exhibited substantial between-

year differences in allelic frequencies at several loci. We believed that these temporal differences could not be reasonably attributed to sampling error, genetic drift, or stock transfers between river systems. Second, when several fishery collections of pink salmon tissues that had been analyzed in-season by one laboratory in 1987 were subsequently reanalyzed by a second laboratory, a considerable number of discrepancies in genotypic scores between the two laboratories were noted. The questionable nature of these past results together with our belief that multilaboratory GSI programs should include evaluation of data consistency prompted the present study.

The PSC designed its 1989 in-season GSI program to facilitate testing the consistency of electrophoretic analyses performed by separate laboratories. Incorporating principles of replication in the experimental design was seen as an effective means of achieving this objective. Shaklee and Phelps (1990) pointed out the potential value of comparing replicated laboratory analyses in multiagency GSI programs because many laboratories contribute and use information from a common database, but they provided no evidence that inconsistencies actually occurred. Hence, the consistency of the electrophoretic analyses conducted for the PSC was tested by having replicate collections of pink salmon tissue samples (that were extracted from the same fish) independently analyzed by up to three different laboratories. Note that the term "replicate" is used in a generic sense throughout this paper to refer to any collections of identical tissue samples that were independently analyzed by two or more laboratories. Some of the laboratory analyses of replicated collections were conducted in a "double-blind" manner. That is, the laboratories had no prior knowledge of which collections were part of the replicate tests (i.e. the collections used for the replicate tests were not distinguished from other collections intended for routine processing) or of the scores obtained by the other laboratories for any of the analyses. In the remaining analyses of replicate collections, one of the laboratories knew which collections were part of the replicate comparisons; however, this laboratory had no knowledge of the scores obtained by the other laboratory for those collections.

The objectives of the analyses in this study were to (1) determine the number and pattern of scoring discrepancies by evaluating sets of scores from replicated analyses of tissue samples for different laboratories, (2) identify probable methodological sources for scoring discrepancies at specific loci, (3) compare the stock composition estimates that were generated for each replicated collection using the scores from different laboratories and explore their fisheries management implications, and (4) recommend procedures to maximize the consistency of electrophoretic data in GSI programs dependent on input from multiple laboratories.

Materials and Methods

Three laboratories (identified in this report as laboratories A, B, and C) were contracted by the PSC to carry out the electrophoretic analysis of pink salmon tissue samples from mixed-stock fishery samples in 1989. All of the laboratories had several years of experience prior to this study conducting electrophoretic analyses of Pacific salmon, including pink salmon. The compilation of the genetic data and execution of the MLE analyses were conducted by PSC staff.

Laboratory Methods

Two weeks before initiating the in-season analyses, staff from all three laboratories participated in an intensive two-day workshop where the following aspects of the project were discussed and standardized: the genetic bases and subunit structures for all enzyme systems to be screened during the fishery analyses, enzyme and locus nomenclature; allele identification and coding; specific electrophoretic techniques such as buffer and enzyme staining recipes and gel running conditions (voltage and amperage settings, temperatures, running times, etc.); recommended screening protocols and methods of gel handling and identification; isozyme scoring conventions and criteria; and data formats. The workshop was also intended to establish a close working relationship between Commission staff and personnel from the laboratories so that if difficulties in the electrophoretic analyses emerged, they could be identified and remedied quickly.

Information concerning the 15 systems (18 loci; counting each isolocus pair as two loci) that were analyzed in this study is summarized in Appendices A and B. Standard methods of horizontal starch–gel electrophoresis and histochemical staining were used (Selander et al. 1971; Harris and Hopkinson 1976; Shaklee and Keenan 1986; Aebersold et al. 1987).

All phenotypic patterns were to be photographed and independently interpreted by at least two individuals in each laboratory, and any within-laboratory scoring discrepancies were to be resolved prior to submitting the final scores to the Commission. This process was recommended to minimize errors in both gel interpretation and data recording. Three additional laboratory procedures were recommended at the workshop to prevent gel-handling mistakes. The first procedure was to notch the corner(s) of each gel differently so that all gels on a specific day were uniquely identified. Provided that each gel was notched at the end where the first sample was loaded, the notches also identified the starting point on each gel and reduced the likelihood that gels would be read backwards. The second procedure was to incorporate "redundant" screening in the electrophoretic protocol by obtaining scores for several loci (i.e. *ALAT**, *G3PDH-1**, *PEPD-2**, and *PGM-2**) from two different gels (see Appendix A). This approach served two purposes. It provided two opportunities to score the enzymes stained on both gels, and thereby would be expected to increase scoring accuracy for these loci. It also provided a means for detecting mistakes in gel loading and handling because it yielded two independent sets of scores (from different gels) for these loci. Thus, if the samples were mistakenly loaded in a different order on the two different gels (different buffers) or if the slices from two or more gels were mixed up, a number of discrepancies between the two sets of scores for the "redundant" loci would be anticipated. The third precaution was to load samples asymmetrically on the gel (e.g. if 45 samples were loaded on each gel, the first 30 samples could be loaded in three groups of 10 samples, each separated by a gap, and the final 15 samples in another group). The resulting asymmetry would clearly indicate which edge was the starting point for scoring each gel slice.

Electrophoretic Analyses to Include Replicate Comparisons

At the workshop, the Commission advised all three laboratories that double-blind, replicate comparisons of tissue collections would be made throughout the fishery analyses. The replicate comparisons were intended to serve two main purposes. First, they were used to assess the consistency of data collected by the three laboratories. Second, they (especially those occurring early in the fishery analyses) were used to identify problem

areas where discrepancy rates for specific loci were high. This would allow attention to be focused on assisting laboratories that were experiencing difficulties with certain loci.

The study consisted of two replicate tests (1 and 2) involving all three laboratories, one two-way replicate test (3) involving only laboratories A and B, and six two-way replicate tests (4–9) involving only laboratories A and C. The details of all nine replicate comparisons are presented in Table 1.

Replicates 1–3 were based on analyses of equivalent/identical tissue samples; that is, a piece of muscle tissue from each fish was subdivided and the resulting subsamples were placed in identically labelled plastic tubes, frozen immediately on dry ice, and shipped on dry ice to each laboratory. In contrast, the tissue samples analyzed in replicate comparisons 4–9 were first homogenized and analyzed by laboratory C, then refrozen, stored at −20°C for up to 3 mo, and eventually reanalyzed by laboratory A. None of the laboratories had prior knowledge of the scores obtained by other laboratories for any of the nine replicate comparison tests.

Analysis and Comparison of Sample Replicates among Laboratories

An unexpected aspect of the in-season field sampling of fisheries in 1989 was the inadvertent inclusion of tissue samples from other species of salmon (presumably due to the participation of an inexperienced member of the field staff). The presence of non-pink salmon tissues in replicate 2 provided an additional, unanticipated test of the gel scoring and interpretation abilities of the three laboratories. If the laboratories were unable to identify these other species, "contamination" of the resulting data sets (Shaklee et al. 1990c) could have occurred.

All of the remaining analyses were focused on the scoring of pink salmon samples only. We identified several types of scoring problems and quantified their rate of occurrence in the replicates. The first was "zero" scores, where no score was recorded for a fish at a specific locus because the laboratory could not determine the score with reasonable confidence. We calculated the zero score rate by dividing the number of zero scores recorded by a laboratory by the total number of scores possible for that collection. Zero scores were considered to be different from actual "discrepancies" because missing data for fishery samples cannot be used in the MLE process to generate estimates of stock composition. However, because zero scores reduce the amount of information available for MLE, they likely decrease the power of the analysis, and hence are undesirable. If missing scores were differentially associated with particular genotypes, they could also contribute to increased bias in stock composition analyses.

We calculated two different types of discrepancy rates for each locus based on scoring disagreements. The variant error rate was the number of scoring discrepancies for "variants" (individuals not homozygous for the common allele at a locus; i.e. not having the **100/100* genotype) divided by the total number of variant scores recorded for a replicate collection. The overall discrepancy rate was the total number of scoring discrepancies divided by the total number of non-zero scores recorded for that replicate collection. The calculation of discrepancy rates for the replicate collections analyzed by only two laboratories (replicates 3–9) was straightforward because there were only two sets of scores for each collection. However, there were several options for calculating discrepancy rates for the two three-way replicates (1 and 2). For example, it would have been possible to calculate three different pairwise discrepancy rates, A versus B, A versus C, and B versus C. To simplify the calculation of discrepancy rates and enable clear interpretation of the results of these replicate comparisons, we chose to compare each laboratory's scores with what we believed to be the correct scores.

We determined what we considered to be the correct scores based on three working assumptions and by analyzing photographs of the isozyme banding patterns taken by the laboratories. The first assumption was that the correct genotype was scored by at least one laboratory. The second was that if the scores from all three laboratories were identical, they were correct. The third assumption was that in cases of scoring disagreements among laboratories, when the scores of two laboratories were in agreement, it was likely that this common score was the correct one. For every discrepancy, gel photographs were analyzed (by J.B.S.) to increase the probability of identifying the correct genotype. The genotype considered to be correct according to the analysis of the photographic records

TABLE 1. Characteristics of the nine replicate collections of pink salmon tissues that were examined in this study.

Replicate	Management area and fishing gear[a]	Lab and date (1989) analyzed			No. of fish in sample
		A	B	C	
1	101 (Tr)	27 July	28 July	27 July	149
2	7A (Ps)	8 Aug.	14 Aug.	11 Aug.	150[b]
3	20 (Ps)	28 Aug.	5 Sept.		149
4	12-3 (Ps)	24 Aug.		28 July	150
5	12-11 (Ps)	23 Aug.		29 July	50[c]
6	20 (Ps)	24 Aug.		21 July	150
7	2W (Ps)	28 Nov.		29 July	150[c]
8	4 (Gn)	29 Nov.		3 Aug.	150
9	142 (Tr)	28 Nov.		2 Aug.	150

[a]The management area codes follow the convention of the Canadian Department of Fisheries and Oceans, with the exception of fishing area "7A," which is designated by the Washington Department of Fisheries. Fishing gear codes are as follows: Tr = troll, Ps = purse seine, Gn = gillnet.

[b]Replicate 2 contained 11 non-pink salmon tissue samples.

[c]Replicates 5 and 7 each contained one non-pink salmon tissue sample.

was also the one scored by two of the three laboratories in all but three cases where all laboratories provided non-zero scores. In these three cases, the genotype scored by only one of the three laboratories was regarded as the correct genotype and the score from the other two laboratories was interpreted as a discrepancy. There were nine cases involving one zero score and two differing scores. In all of these cases, discrepancies were attributed to one or the other laboratory based on the photographic records. No instances were observed where the genotype scored from the photographs differed from scores reported by all three laboratories.

Effect of Differing Genotype Scores on Stock Contribution Estimates

We used an MLE algorithm developed by Fournier et al. (1984) to produce stock composition estimates from the replicate electrophoretic scores provided by the laboratories. The allocate-sum approach (Wood et al. 1987) of combining the contributions of stocks into stock groups after MLE analysis was used. MLE estimates were bootstrapped 50 times and the means according to stock group were reported and compared among the laboratory replicates. MLE estimates were not calculated for replicate 5 because the sample size (50 fish) was considered too small to produce a reliable estimate of stock composition.

Two different baselines were used in the MLE analyses. The first baseline included 38 pink salmon stocks from four major stock groups: (1) Fraser River, (2) Puget Sound, (3) Canada South Coast, and (4) Canada North Coast (Canadian stocks located north of Cape Caution) (Fig. 1; Appendix C). This baseline included data for 10 genetic systems (13 loci, see Appendix B) and was used for analyzing replicates 1, 7, 8, and 9, which had been collected from fisheries occurring north of Cape Caution.

The second baseline, which included data for all 15 genetic systems (18 loci), comprised the 17 Fraser River, Puget Sound, and Canada South Coast stocks also included in the first baseline (but excluded stocks from the Canada North Coast stock group). Laboratory replicates 2, 3, 4, and 6 were obtained from fisheries south of Cape Caution, and therefore were analyzed with this 17-stock baseline. The removal of stocks from the baseline that have a very low probability of being present in the fishery mixtures (because of geographical remoteness or run timing) is expected to reduce bias in the stock composition estimates (Shaklee and Phelps 1990).

Results

Ability of Laboratories to Identify Non-Pink Salmon Samples

Mistakes in the identification of pink salmon during field sampling of fishery catches resulted in the inclusion of 11 non-pink salmon tissue samples in replicate 2. All three laboratories correctly identified these 11 tissue samples as being from species other than pink salmon. Therefore, these fish were excluded from the genetic data files that were used to generate fishery estimates. Our subsequent, postseason electrophoretic analyses of these 11 unknown tissue specimens alongside tissue standards from known specimens of five Pacific salmon species and steelhead revealed that seven were chinook salmon (*Oncorhynchus tshawytscha*), three were coho salmon (*O. kisutch*), and one was a steelhead (*O. mykiss*).

Analysis and Comparison of Scores from Replicates

Laboratory replicate 1 consisted of tissue samples from 149 fish caught north of the Queen Charlotte Islands. These samples were scored at 15 different genetic systems (Table 2). This resulted in a total of 2235 possible scores (149 × 15) by each laboratory and a total of 6705 possible scores for the three laboratories combined. There were a total of 321 variants (i.e. non-**100/100* genotypes) reported for this replicate (out of the 2235 potential scores for each laboratory). All of these variants were confirmed by the isozyme patterns in the gel photographs. Two loci (*LDH-A1** and *sMDH-B1,2**) exhibited no variants while *PEP-LT** and *PEPD-2** each showed over 50 variants. Laboratory A was unable to obtain five scores (out of the possible 2235) for a zero scoring rate of 0.22%, while laboratory B had eight zero scores (0.36%) and laboratory C had 37 zero scores (1.66%) (Table 3). Based on our analysis of both the pattern of score reporting and the photographic records: laboratory A had two scoring discrepancies (variant discrepancy rate of 2/321 = 0.6% and an overall discrepancy rate of 2/2230 = 0.09%); laboratory B had three scoring discrepancies (variant discrepancy rate of 3/321 = 0.9% and an overall discrepancy rate of 3/2227 = 0.13%); and laboratory C had 138 scoring discrepancies (variant discrepancy rate of 138/321 = 43.0% and an overall discrepancy rate of 138/2198 = 6.28%). Statistical evaluation of the numbers of discrepancies in laboratory replicate 1 using a chi-square test showed significant overall heterogeneity among the three laboratories ($\chi^2_{df=2} = 257$; $P << 0.01$). A second test comparing the numbers of discrepancies by laboratories A and B revealed that they were not significantly different ($\chi^2_{df=2} = 0.73$; $P > 0.70$). Rather, the scores from laboratory C were the source of the significant ($P << 0.01$) among-laboratory difference.

Detailed examination of the gel photographs and of the pattern of scores reported by laboratory C compared with those tabulated by the other two laboratories showed that two gel-handling mistakes accounted for 38.4% (53/138) of its discrepancies in scoring variants. One of these mistakes was that two gels (50 fish on each gel) were interchanged so that scores at the three loci scored on these gels by laboratory C (*GPI-A**, *HAGH**, and *PGM-2**) were out of phase (by 50 samples) with the identification number for the correct fish. This mistake resulted in 47 scoring discrepancies. The second mistake was that one of the gels stained for PGM was read backwards (from position 50 to 1 instead of from 1 to 50), resulting in six additional discrepancies at *PGM-2**. These 53 discrepancies resulted from mistakes in gel labelling/handling and not from misinterpretation of isozyme banding patterns (which is perhaps the most common source of error in most electrophoretic studies). However, these 53 discrepancies were of concern because the entire multilocus genotype of each fish in the fishery sample is used in the determination of stock contributions. In this regard, errors in gel handling are likely to decrease the accuracy of the resulting MLE stock contribution estimates.

Two loci, *PEPD-2** and *ALAT**, accounted for two thirds of the discrepancies because of presumed differences in interpretation among the laboratories. Analysis of the gel photographs from replicate 1 indicated two probable sources for the majority of the discrepancies due to the presumed misinterpretation of isozyme patterns by laboratory C. The first problem was that the isozymes had not migrated far enough from the sample origin, apparently because the gels had not been run for long enough or at a sufficently high voltage. This resulted in limited

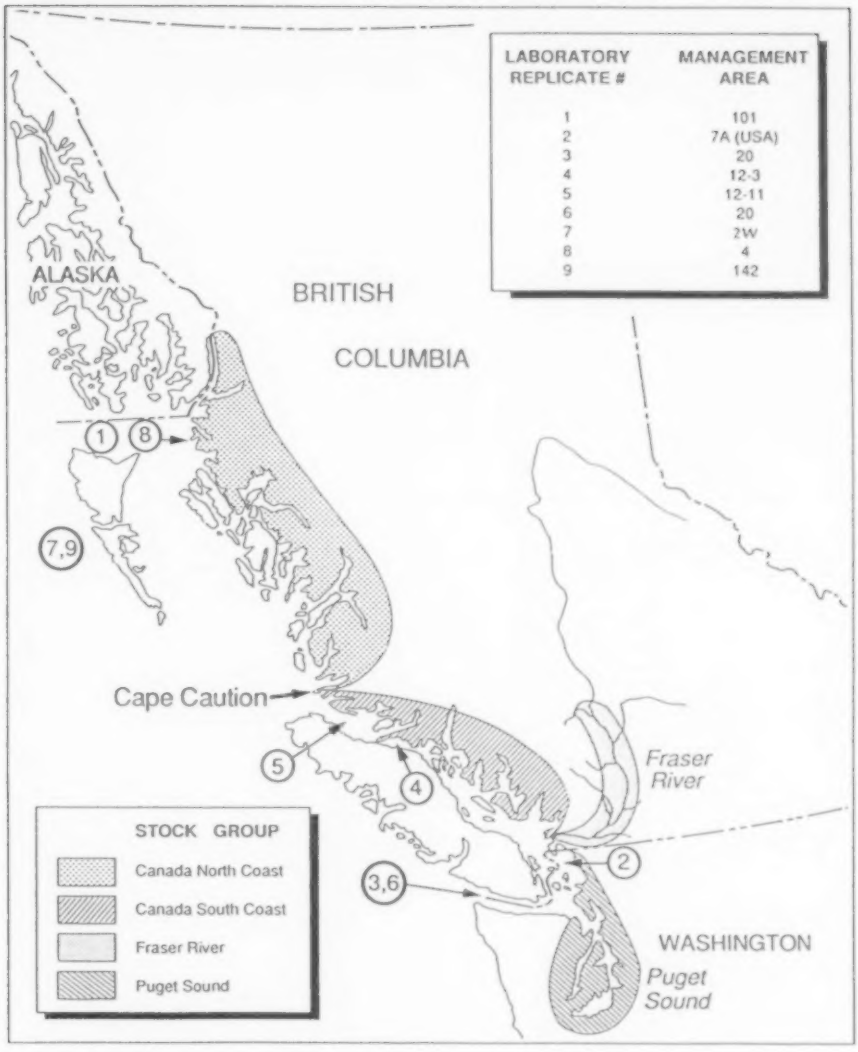


FIG. 1. Map showing locations of the nine laboratory replicate collections (1–9), international boundaries, and Cape Caution (the dividing point between the Canada South Coast and Canada North Coast stock groups). The correspondence between replicates and fishery management areas is shown in the inset.

separation of the isozyme bands for several systems (e.g. ADA-2, ALAT, CK-A1, GPI-B1,2, LDH-A1, PEPD-2, PEP-LT, and PGDH), making scoring difficult.

The second likely source of scoring discrepancies in replicate 1 was weak staining for several enzyme systems (e.g. ADA-2, ALAT, PEPD-2, and PEP-LT) on laboratory C's gels. This interpretation is supported by the observation that this laboratory had higher discrepancy rates for three or more loci for fish scored as heterozygotes than it did for fish scored as homozygotes, in comparison with the other two laboratories. For example, at *ALAT**, 11 of the 13 discrepancies were for fish scored as heterozygotes by the other two laboratories, at *PEPD-2**, 40 of the 44 discrepancies were for heterozygotes, and at *ADA-2** and *PEP-LT**, all discrepancies (five and six, respectively) were for fish scored as heterozygotes by the other two laboratories.

To help laboratory C reduce its discrepancy rate to the level of laboratories A and B, the Commission immediately provided them with the results of the comparative analysis of scores from replicate 1, along with numerous recommendations for enhancing electrophoretic resolution and enzyme staining, and for minimizing problems in gel handling and scoring. Replicate 2 provided the first opportunity to determine if this additional assistance was successful in helping laboratory C to reduce its discrepancy rates.

Replicate 2 consisted of tissue samples from 139 pink salmon caught in the Strait of Georgia. These samples were analyzed for the same loci as replicate 1, yielding a total of 2085 scores by each laboratory. A total of 260 variant genotypes were present in this collection (Table 2). The number of variants ranged from zero at *sMDH-A1,2** and *mMEP-1** to 60 at *PGDH**.

TABLE 2. Discrepancies in scoring variant phenotypes at 18 loci in replicates 1 and 2.

Locus	No. of variants	No. of discrepancies		
		Lab A	Lab B	Lab C
Replicate 1 (149 fish)				
ADA-2	27	1	0	5
ALAT	18	0	0	13
CK-A1	1	0	1	0
GPI-A	7	0	0	10[3][a]
GPI-B1,2	1	0	0	3
G3PDH-1	17	0	0	2
HAGH	16	0	0	18[2][a]
LDH-A1	0	0	0	0
sMDH-A1,2	0	1	1	0
sMDH-B1,2	24	0	0	3
mMEP-1	7	0	0	1
PEPD-2	91	0	0	44
PEP-LT	59	0	1	6
PGDH	34	0	0	1
PGM-2	19	0	0	32[2][a]
Totals	321	2	3	138[85][a]
Replicate 2 (139 fish)[b]				
ADA-2	21	2	1	1
ALAT	36	1	4	19
CK-A1	1	0	0	0
GPI-A	1	0	0	0
GPI-B1,2	8	0	1	0
G3PDH-1	17	0	0	0
HAGH	13	0	1	1
LDH-A1	5	0	0	0
sMDH-A1,2	0	0	0	1
sMDH-B1,2	5	1	1	1
mMEP-1	0	0	0	0
PEPD-2	49	0	0	0
PEP-LT	7	0	0	4
PGDH	60	0	0	2
PGM-2	37	1	0	0
Totals	260	5	8	29

[a]Numbers in square brackets represent discrepancies after correction for presumed mistakes of gel plating (all three loci) and reading from back to front (*PGM-2* only) (see text).

[b]An additional 11 fish were in this collection but they were non-pink salmon species and are omitted from this summary (see text).

Laboratory A had two zero scores and five variant discrepancies (1.9% variant discrepancy rate), laboratory B had one zero score and eight variant discrepancies (3.1% variant discrepancy rate), and laboratory C had 71 zero scores and 29 variant discrepancies (11.2% variant discrepancy rate) (Table 3). The overall discrepancy rates of laboratories A and B remained low (<0.40%) in this replicate, while that of laboratory C was 1.44%.

The discrepancy rates associated with laboratory C decreased considerably from replicate 1 to 2 at several loci. The greatest improvement was at *PEPD-2** where the discrepancy rate dropped from over 29.5% (44 discrepancies/149 fish) to zero. These decreases in discrepancy rates suggested that the recommendations provided to laboratory C (based on the results from replicate 1) were beneficial. However, the overall discrepancy rate of laboratory C remained over three and a half times higher than that of laboratory A or B and was the source of the significant difference in error rates observed in this replicate ($\chi^2_{df=2} = 24.4$; $P < 0.01$). Nearly two thirds of their discrepancies in replicate 2 were at the *ALAT** locus.

TABLE 3. Summary of zero score rates, variant discrepancy rates, and overall discrepancy rates in replicates 1–3. Note that laboratory C was not involved in replicate 3.

	% zero scores			% variant discrepancies			% overall discrepancies		
	1	2	3	1	2	3	1	2	3
Lab									
A	0.22	0.10	0.18	0.6	1.9	0.4	0.09	0.24	0.04
B	0.36	0.05	0.00	0.9	3.1	3.2	0.13	0.38	0.36
C	1.66	3.41	n/a	43.0	11.2	n/a	6.28	1.44	n/a

The proportion of zero scores reported by laboratory C more than doubled from replicate 1 (1.66%) to replicate 2 (3.41%). In replicate 2, their zero-score rate was approximately 35 times higher than that recorded by laboratory A or B. This loss of information would likely reduce the power of the MLE stock composition analyses.

Replicate 3 involved tissue samples from 149 pink salmon caught in Juan de Fuca Strait. This two-laboratory replicate was analyzed by laboratories A and B at 15 systems and yielded a total of 2235 scores by each laboratory. Laboratory A had 4 zero scores (0.18%), while laboratory B had none. There were nine discrepancies between the scores from the two laboratories. Analysis of the scores and accompanying gel photographs showed that one of these nine discrepancies was due to a scoring mistake by laboratory A (yielding a variant discrepancy rate of 0.4% and an overall discrepancy rate of 0.04%), while eight were due to scoring mistakes by laboratory B (variant discrepancy rate of 3.2% and an overall discrepancy rate of 0.36%). As was the case in replicates 1 and 2, laboratories A and B had close agreement between their scores in this replicate.

Laboratories A and B exhibited consistently low overall discrepancy rates in all three replicates (<0.40% in all cases). The higher discrepancy rates associated with laboratory C in replicates 1 and 2 suggested that the scores from other fishery collections originally analyzed by laboratory C might also potentially exhibit higher discrepancy rates when compared with scores from either of the other two laboratories. To examine this concern further, laboratory A (the laboratory with the lowest discrepancy rates in replicates 1–3) was chosen by the Commission to reanalyze six fishery collections originally processed by laboratory C.

The reanalysis of these six collections formed the basis for the six additional laboratory replicate comparisons (4–9; Table 1) described below. These collections consisted of a total of 794 scorable pink salmon tissue samples (i.e. of the 800 fish in these collections, two fish were non-pink salmon and four of the tissue samples were unscorable). Laboratory A scored these samples for all 15 systems analyzed in the first three replicates, while laboratory C did not score *LDH-A1** and *PGM-2* in one collection, HAGH** in another collection, or *ALAT** in a third collection. Therefore, the total number of comparable scores by the two laboratories combined was 22 628. Labora-

tory C had a total of 390 (1.72%) zero scores during its initial screening of these collections (excluding the 596 missing scores for the four loci listed above), while laboratory A had 259 zero scores (1.15%) during its subsequent analysis of these samples. The unusually large number of zero scores recorded by laboratory A for these collections (compared with the number of zero scores reported by this laboratory in replicates 1–3) is probably at least partially attributable to the fact that the tissue samples from these six collections had all been previously thawed, homogenized, and refrozen by the other laboratory. This double-handling of the tissue samples would have increased the difficulty of interpreting the electrophoretic patterns for laboratory A because of enzyme breakdown. Aebersold et al. (1987) noted that enzyme degradation in salmon tissue samples is apparent after a few weeks of storage at −10 to −20°C. Because the tissue samples for collections 4–9 had all been stored at (−20°C) for 25 or more days before reanalysis, it is probable that this storage (and the extra thawing and refreezing) of these samples resulted in significant enzyme degradation, making scoring more difficult or impossible in some cases.

A total of 260 scoring discrepancies were observed out of the 10 665 pairs of scores reported ((22 628 possible scores − 2 × (649 zero scores))/2) by the two laboratories. This yielded an average overall discrepancy rate of 2.44% (assuming that only one score of each pair was incorrect). The average variant discrepancy rate of these six replicates was 16.5%, from a total of 1571 variants that were present. These observations for the final six replicate comparisons supported the Commission's concern that the fishery collections originally processed by laboratory C could have a higher discrepancy rate associated with them.

Comparison of Stock Composition Estimates Using Replicate Scores from Different Laboratories

A wide range of differences among the laboratories in the estimated contributions of stock groups to the fishery mixtures was apparent following MLE analysis of the data from eight of the replicate collections (Table 4). Recall that MLE estimates were not calculated for replicate collection 5 because of its small sample size. Stock group estimates produced from the scores provided by laboratories A and B agreed closely for all three replicates where they were compared (1–3). On average, the amount that the stock group estimates varied between laboratories A and B was approximately 1%. The largest difference in estimates seen between these two laboratories occurred in replicate 3 where a 3% difference in estimates of the Canada South Coast stock group was observed (i.e. 12 versus 9%). Because of the close similarity in stock contribution estimates between laboratories A and B, the remainder of the comparison focused on examining the MLE estimates produced from scores provided by laboratory C.

Comparison of the MLE results obtained using the scores reported by laboratories A and C (Table 4) indicated that many estimates differed considerably. The actual differences in individual stock group estimates obtained using scores from laboratories A and C varied from 0% (e.g. replicate 7, Fraser River stock group) to a high of 30% (49 versus 19%, replicate 4, Puget Sound stock group). For the Fraser River stock group, the difference in the MLE estimates from laboratories A and C varied from 0 to 14%. The average difference in all of the stock group estimates across all seven of the replicate comparisons involving laboratories A and C was approximately 8%. The closest agreement in the estimates from these two laboratories was seen in replicate 8, where the mean difference in the stock group estimates was 2%. The largest differences in average stock group estimates between the two laboratories was 20%, which occurred in replicate 4.

TABLE 4. Comparison of stock composition estimates for eight replicate collections using data from different laboratories.

		Estimated contribution by stock group (%)			
Replicate	Lab	Fraser River	Puget Sound	Canada South Coast	Canada North Coast
1	A	2	0	9	89
	B	4	0	7	89
	C	5	16	3	76
2	A	64	29	7	n/a
	B	64	30	6	n/a
	C	74	19	7	n/a
3	A	48	40	12	n/a
	B	50	41	9	n/a
4	A	40	19	41	n/a
	C	26	49	25	n/a
6	A	39	55	6	n/a
	C	34	49	17	n/a
7	A	3	7	15	75
	C	3	29	6	62
8	A	0	3	2	95
	C	0	0	1	99
9	A	34	6	2	58
	C	28	11	3	58

We also calculated the mean and range of standard errors of estimates by stock group. The standard error of the estimates varied from 0 to 19% (mean standard error was 9%). Determining the variance of specific GSI estimates is useful for establishing the confidence that should be associated with particular estimates. However, for fisheries management, the importance of the variance (or precision) of estimates is often secondary to the accuracy of the estimates. This is because the mean point estimates by stock or stock group are generally one of the key variables used for fisheries management and catch allocation.

Discussion

Although GSI can be a powerful tool for determining the contributions of stocks in mixed-stock fisheries of Pacific salmon (Shaklee et al. 1990b), there are several potential problems in applying the technique. Complications that can seriously compromise the success of such programs can arise during baseline creation, in-season fishery sampling, electrophoretic analyses, and statistical analysis of the genetic data.

The reliability of laboratory analyses in GSI studies is critical because important management decisions regarding economically and biologically valuable fish stocks often depend on such data. Many GSI fishery programs in North America now use shared databases containing results from different laboratories. In such cases, the contribution of inconsistent electrophoretic

data from a laboratory could potentially compromise all fishery (and other) analyses using this baseline database. For a number of reasons, it is becoming increasingly important that GSI studies focus more attention on data accuracy and compatibility: (a) MLE analysis of fishery composition is sensitive to errors in gel scoring; (b) the numbers of loci and alleles now used in most GSI studies are much larger than in the past and many of the associated isozyme patterns are complex and difficult to interpret (Shaklee and Phelps 1990); and (c) the amount of genetic differentiation among many of the stocks or stock groups of management interest is sometimes low, and therefore the genotypic scores must be as accurate as possible to enable discrimination of these similar groups.

Four principal conclusions can be drawn from the current study of interlaboratory consistency in electrophoretic analyses. First, electrophoretic analyses of pink salmon muscle tissue samples by independent laboratories can provide consistent (and presumably accurate) determinations of individual fish genotypes. Judging from the results of the present study, overall discrepancy rates can be consistently less than 0.40% (e.g. laboratories A and B had overall discrepancy rates ranging from 0.04 to 0.38% in replicates 1–3). These discrepancy rates resulted in an average difference of 1% in the estimated stock group contributions for the three replicates. This small difference in the stock contribution estimates is within acceptable limits for most fisheries management requirements and is probably less than the error contributed by other steps in the mixed-stock fishery analysis process.

The second major finding of this study is that laboratories may report electrophoretic data that is inconsistent with data obtained by other laboratories analyzing equivalent tissue samples from the same fish. The use of data with high discrepancy rates may lead to unreliable stock composition estimates. The average difference in the stock group estimates between the laboratories with the lowest and highest discrepancy rates for seven replicate comparisons was 8% (range 0–30%).

The use of unreliable or inaccurate stock composition estimates could be expected to adversely affect the ability of fisheries managers to fulfill their responsibilities. Although fisheries agencies applying GSI likely having differing requirements for reliability and accuracy in their stock composition estimates (based on different management needs), it is probable that the goals of many agencies would be compromised by estimates that varied up to the amount observed in the current study (stock group estimates varied by an average of 20% in replicate 4).

The primary management goals of the Fraser River Panel of the PSC for Fraser River pink salmon are achieving escapement goals and international and domestic allocation of catches between user groups (PSC 1989). Examination of stock group estimates in Table 4 suggests that there may have been a bias in analyses using scores from the laboratory with the highest discrepancy rate that led to overestimation of pink salmon from the Puget Sound stock group and underestimation of the other stock groups, including Fraser River pink salmon in the fishery mixtures. Underestimation of the contribution of Fraser River pink salmon in the mixed-stock fisheries could result in inadvertently overharvesting Fraser River stocks because many fish would have been incorrectly identified as pink salmon from other stock groups. If the run sizes were not substantially larger than the preseason forecast, this could compromise achieving the escapement goal for Fraser River pink salmon stocks.

The appropriate international and domestic allocation of catches between fishermen from the United States and Canada would also be compromised by failing to accurately estimate the contributions of Fraser River pink salmon in commercial fisheries when they are present. If the forecasted run of Fraser River pink salmon was of the size anticipated, but GSI underestimated their contribution to the fisheries, specific fishermen/user groups from one or both countries may not receive the share of the catch that was allocated to them before the season. This situation might require significant, and unwarranted, "pay-backs" of catches of Fraser River pink salmon in future years to one or more user groups.

The Fraser River Panel of the PSC applied GSI to the analysis of approximately 27 million pink salmon that were caught in various fisheries in 1989. If even 5–10% of these fish were misidentified during the 1989 season as a result of incorrect stock composition analyses, this would result in the misallocation of between 1.35 and 2.70 million fish. Misallocation of this many pink salmon would have an unfavourable effect on achieving the management goals described above.

Our third conclusion is that replicate comparisons can be used to identify methodological sources of discrepancies by particular laboratories (e.g. problems in gel handling) and promote measures to remedy them. In the present study, it was encouraging that after the laboratory with the highest discrepancy rate associated with its scores received additional assistance, its overall discrepancy rate decreased over fourfold in the following replicate comparison (i.e. from 6.28% in replicate 1 to 1.44% in replicate 2).

Our fourth conclusion, which follows from the second and third conclusions, is that future multilaboratory GSI programs should be organized to include replicate comparisons. Several important design and operational components of large-scale, multiagency GSI programs have been outlined previously (e.g. Shaklee 1983, 1988; Shaklee and Phelps 1990). One recommendation was for "blind testing" of replicate samples to confirm consistency in gel scoring between electrophoretic laboratories. The current study provides strong empirical evidence of the need for adopting this recommendation.

The practice of comparing the results of replicated analyses is common in other laboratory technologies, and it is apparent that such evaluations should also be included in GSI applications. Replicate tests are commonly used in forensic, inspection, and regulatory types of analysis and are often used either as part of a laboratory certification process or as a means of improving the accuracy and comparability of data collection and interpretation conducted by multiple, independent laboratories (Learson 1969, 1970; Lundstrom 1980, 1983).

Despite the greater work involved in coordinating and standardizing the electrophoretic analyses of several laboratories for the same GSI program, there can be additional benefits beyond confirming data reliability. Many GSI programs require the results of analyses on a rapid basis so that regulations for management of commercial fisheries can be developed, and if necessary modified, in-season. By employing multiple laboratories in GSI programs, the laboratory processing rate for tissue samples is increased, thereby reducing the turnaround time that is needed for fisheries managers to receive stock composition estimates. Additionally, by enlisting as many laboratories in GSI studies as is logistically and economically possible, the overall pool of trained personnel for conducting future electrophoretic analyses is enlarged.

There are several factors that should be considered when deciding on the number and deployment of replicates in a GSI program. The primary economic consideration involving replicates is that because they require duplicating specific analyses among two or more laboratories, they represent an increase in cost for those analyses. However, in large-scale GSI programs the proportion of analyses involving replicate comparisons can be small (e.g. approximately 8% in this study, counting all nine collections analyzed by two or more laboratories) and still provide a powerful check on the reliability of the analyses. Although the replicates should be distributed throughout the sampling period in a manner that conforms to acceptable sampling standards, it is advisable to schedule one of the replicates among the earliest sample collections so that steps can be taken to correct any problems encountered before they compromise subsequent analyses. We recommend that replicates be included for mixed-stock fishery samples from a wide geographic range so that consistency in scoring of the full array of possible biochemical phenotypes can be assessed among the laboratories. Because a primary goal of GSI studies should be data consistency and accuracy, we also recommend that replicate testing include the generation and analysis of photographic records. Finally, multiagency GSI programs should maintain an ongoing schedule of replicate testing, even after two or more laboratories have shown they can provide consistent results. This is important because of the dynamic nature of GSI programs and techniques (i.e. year-to-year changes in laboratory personnel, analytical conditions, and the loci and alleles that are analyzed).

Shaklee and Phelps (1990) noted many coordination and standardization steps, in addition to replicates, that should be followed to promote the collection of accurate and compatible GSI data. These procedures included scheduling interlaboratory meetings and workshops, sharing electrophoretic and staining methodologies, developing uniform systems of enzyme, locus, and allele nomenclature, adopting and using common data formats, and exchanging and using allele mobility standards.

Many fisheries agencies in the Pacific northwest currently participate in an informal, coastwide consortium for salmon GSI intended to facilitate the standardization and coordination measures described above. Major participants include the U.S. National Marine Fisheries Service laboratories in Seattle and Auke Bay, the PSC, the Canadian Department of Fisheries and Oceans, the University of California at Davis (and California Department of Fish and Game), the U.S. Fish and Wildlife Service Laboratory at Anchorage, and the Washington Department of Fisheries. In the past six years, this group has made substantial progress in coordination and standardization of GSI studies for chinook, chum (*Oncorhynchus keta*), and pink salmon.

A positive finding of this study was the confirmation that independent electrophoretic laboratories can obtain consistent, and presumably accurate, results. However, our finding that data may be reported which are inconsistent with data collected by other laboratories on equivalent samples provides some justification for reexamining the results of previous GSI studies where questionable data may have been reported, especially where such data are still being used for fisheries analyses. We believe that the replication procedures employed in this study can and should be applied in ongoing and future GSI programs, including those employing nuclear and mitochondrial DNA analysis.

Future research should address some of the other complications to GSI programs, such as developing a method of reducing bias in the stock contribution estimates produced from the maximum likelihood estimation process. Another problem is defining and obtaining sufficiently large and representative collections of tissue samples from mixed-stock fisheries (and baselines) to characterize their genetic composition accurately. We believe that further improvements in the accuracy of GSI estimates will be achieved through the cooperative efforts of the many agencies and laboratories applying this powerful technique on the Pacific coast.

Acknowledgments

We thank all field samplers and laboratory personnel who contributed to the analyses described in this report. We also thank Ian Todd, Jim Woodey, Jim Gable, Steve Cox-Rogers, and Craig Busack for their helpful comments on the manuscript. This study was conducted with funds from the Pacific Salmon Commission and the State of Washington General Fund.

References

AEBERSOLD, P. B., G. A. WINANS, D. J. TEEL, G. B. MILNER, AND F. M. UTTER. 1987. Manual for starch gel electrophoresis: a method for the detection of genetic variation. NOAA Tech. Rep. NMFS 61: 19 p.

ALTUKHOV, YU. P. 1981. The stock concept from the viewpoint of population genetics. Can. J. Fish. Aquat. Sci. 38: 1523–1528.

BARTLEY, D. M., AND G. A. E. GALL. 1990. Genetic structure and gene flow in chinook salmon populations of California. Trans. Am. Fish. Soc. 119: 55–71.

BEACHAM, T. D., R. E. WITHLER, AND A. P. GOULD. 1985a. Biochemical genetic stock identification of pink salmon (*Oncorhynchus gorbuscha*) in southern British Columbia and Puget Sound. Can. J. Fish. Aquat. Sci. 42: 1474–1483.

1985b. Biochemical genetic stock identification of chum salmon (*Oncorhynchus keta*) in southern British Columbia. Can. J. Fish. Aquat. Sci. 42: 437–448.

BEACHAM, T. D., R. E. WITHLER, C. B. MURRAY, AND L. W. BARNER. 1988. Variation in body size, morphology, egg size, and biochemical genetics of pink salmon in British Columbia, Trans. Am. Fish. Soc. 117: 109–126.

CLAYTON, J. W., AND D. N. TRETIAK. 1972. Amine-citrate buffers for pH control in starch gel electrophoresis. J. Fish. Res. Board Can. 29: 1169–1172.

FERRIS, S. D., AND G. S. WHITT. 1978. Genetic and molecular analysis of nonrandom dimer assembly of the creatine kinase isozymes of fishes. Biochem. Genet. 16: 811–829.

FOURNIER, D. A., T. D. BEACHAM, B. E. RIDDELL, AND C. A. BUSACK. 1984. Estimating stock composition in mixed stock fisheries using morphometric, meristic, and electrophoretic characteristics. Can. J. Fish. Aquat. Sci. 41: 400–408.

GHARRETT, A. J., S. M. SHIRLEY, AND G. R. TROMBLE. 1987. Genetic relationships among populations of Alaskan chinook salmon (*Oncorhynchus tshawytscha*). Can. J. Fish. Aquat. Sci. 44: 765–774.

HARRIS, H., AND D. A. HOPKINSON. 1976. Handbook of enzyme electrophoresis in human genetics. American Elsevier Publ. Co., New York, NY.

HOLMES, R. S., AND C. J. MASTERS. 1970. Epigenetic interconversions of the multiple forms of mouse liver catalase. FEBS Lett. 11: 45–48.

JOHNSON, K. R. 1979. Genetic variation in populations of pink salmon (*Oncorhynchus gorbuscha*) from Kodiak Island, Alaska. M.S. thesis, University of Washington, Seattle, WA.

KUTKUHN, J. H. 1963. Estimating absolute age composition of California salmon landings. Calif. Dep. Fish Game Fish Bull. 120: 42 p.

LEARSON, R. J. 1969. Collaborative study of a rapid electrophoretic method for fish identification. J. Assoc. Off. Anal. Chem. 52: 703–707.

1970. Collaborative study of a rapid electrophoretic method for fish identification. II. Authentic flesh standards. J. Assoc. Off. Anal. Chem. 53: 7–9.

LEARY, R. F., F. W. ALLENDORF, S. R. PHELPS, AND K. L. KNUDSEN. 1987. Genetic divergence and identification of seven cutthroat trout subspecies and rainbow trout. Trans. Am. Fish. Soc. 116: 580–587.

LOUDENSLAGER, E. J., AND G. A. E. GALL. 1980. Geographic patterns of protein variation and subspeciation in the cutthroat trout. Syst. Zool. 29: 27–42.

LUNDSTROM, R. C. 1980. Fish species identification by thin layer polyacrylamide gel isoelectric focusing: collaborative study. J. Assoc. Off. Anal. Chem. 63: 69–73.

1983. Fish species identification by agarose gel isoelectric focusing: collaborative study. J. Assoc. Off. Anal. Chem. 66: 123–127.

MCGREGOR, A. J. 1983. A biochemical genetic analysis of pink salmon (*Oncorhynchus gorbuscha*) from selected streams in northern southeast Alaska. Alaska Dep. Fish Game Inf. Leafl. 213.

OKAZAKI, T. 1982. Genetic study on population structure in chum salmon (*Oncorhynchus keta*). Bull. Far Seas Fish. Res. Lab. 19: 25–116.

PACIFIC SALMON COMMISSION (PSC). 1989. Report of the Fraser River Panel to the Pacific Salmon Commission on the 1988 Fraser River sockeye salmon fishing season. 600-1155 Robson Street, Vancouver, B.C. 38 p.

PELLA, J. J., AND G. B. MILNER. 1987. Use of genetic marks in stock composition analysis, P. 247–276. *In* N. Ryman and F. M. Utter [ed.] Population genetics and fishery management. University of Washington Press, Seattle, WA.

RYMAN, N., F. W. ALLENDORF, AND G. STAHL. 1979. Reproductive isolation with little genetic divergence in sympatric populations of brown trout (*Salmo trutta*). Genetics 92: 247–262.

SELANDER, R. K., M. H. SMITH, S. Y. YANG, W. E. JOHNSON, AND J. B. GENTRY. 1971. Biochemical polymorphism and systematics in the genus *Peromyscus*. I. Variation in the old field mouse (*Peromyscus polionotus*). Stud. Genet. IV Univ. Tex. Publ. 7103: 49–90.

SHAKLEE, J. B. 1983. The utilization of isozymes as gene markers in fisheries management and conservation, p. 213–247. *In* M. C. Rattazzi, J. G. Scandalios, and G. S. Whitt [ed.] Isozymes: current topics in biology and medicine. Vol. 11. Academic Press, New York, NY.

1988. GSI standardization, coordination, documentation, and validation, p. 20–22. *In* R. Lincoln [ed.] Summary of a seminar on genetic stock identification (GSI) of chinook salmon: status, needs and future. Report TCCHINOOK (88)-1 of Joint Chinook Technical Committee, Pacific Salmon Commission, 600-1155 Robson Street, Vancouver, B.C.

SHAKLEE, J. B., F. W. ALLENDORF, D. C. MORIZOT, AND G. S. WHITT. 1990a. Gene nomenclature of protein-coding loci in fish. Trans. Am. Fish. Soc. 119: 2–15.

SHAKLEE, J. B., C. BUSACK, A. MARSHALL, M. MILLER, AND S. R. PHELPS. 1990b. The electrophoretic analysis of mixed-stock fisheries of Pacific salmon, p. 235–265. *In* Z-I. Ogita and C. L. Markert [ed.] Isozymes: structure, function and use in biology and medicine. Progress in clinical and biological research. Vol. 344. Wiley-Liss Inc., New York, NY.

SHAKLEE, J. B., AND C. P. KEENAN. 1986. A practical laboratory guide to the techniques and methodology of electrophoresis and its application to fish fillet identification. CSIRO Rep. Aust. 177: 59 p.

SHAKLEE, J. B., AND S. PHELPS. 1990. Operation of a large-scale, multiagency genetic stock identification program. Am. Fish. Soc. Symp. 7: 817–830.

SHAKLEE, J. B., S. R. PHELPS, AND J. SALINI. 1990c. Analysis of fish stock structure and mixed-stock fisheries by the electrophoretic characterization of allelic isozymes, p. 173–196. *In* D. H. Whitmore [ed.] Applications of electrophoresis and isoelectric focusing techniques in fisheries management. CRC Press, Boca Raton, FL.

STAHL, G. 1981. Genetic differentiation among natural populations of Atlantic salmon (*Salmo salar*) in northern Sweden, p. 95–105. *In* N. Ryman [ed.] Fish gene pools. Ecological Bulletins. Vol. 34. Stockholm, Sweden.

STEER, G. J., N. B. F. COUSENS, H. STIFF, AND K. D. HYATT. 1986. An analysis of gear selectivity and sources of bias in estimates of age and stock composition of the 1980–1984 Barkley Sound sockeye salmon (*Oncorhynchus nerka*) catch. Can. Tech. Rep. Fish. Aquat. Sci. 1445: 77 p.

TOMLINSON, P. K. 1971. Some sampling problems in fishery work. Biometrics 27: 631–641.

UTTER, F., F. W. ALLENDORF, AND B. MAY. 1979. Genetic basis of creatine kinase isozymes in skeletal muscle of salmonid fishes. Biochem. Genet. 17: 1079–1091.

UTTER, F., G. MILNER, G. STAHL, AND D. TEEL. 1989. Genetic population structure of chinook salmon, *Oncorhynchus tshawytscha*, in the Pacific Northwest. Fish. Bull. U.S. 87: 239–264.

UTTER, F., D. TEEL, G. MILNER, AND D. MCISAAC. 1987. Genetic estimates of stock compositions of 1983 chinook salmon harvests off the Washington Coast and the Columbia River. Fish. Bull. U.S. 85: 13–23.

WHITMORE, D. H. [ED.] 1990. Applications of electrophoresis and isoelectric focusing techniques in fisheries management. CRC Press, Boca Raton, FL.

WOOD, C. C., S. MCKINNELL, T. J. MULLIGAN, AND D. A. FOURNIER. 1987. Stock identification with the maximum-likelihood mixture model: sensitivity analysis and application to complex problems. Can. J. Fish. Aquat. Sci. 44: 866–881.

Appendices

APPENDIX A. Enzyme and locus nomenclature[a] and electrophoretic screening conditions for pink salmon GSI using muscle tissue.

Locus[a]	Synonomy[b]	Enzyme name (No.)	Subunit structure[c]	Buffer (s)[d]
ADA-2	Ada (Ada-2)	Adenosine deaminase (3.5.4.4)	M	CAME6.3
ALAT		Alanine aminotransferase (2.6.1.2)	D	TRIS–GLY and CAME6.3
CK-A1	Ck-1	Creatine kinase (2.7.3.2)	D[e]	TRIS–GLY
GPI-A	Pgi-3 (Phi-3)	Glucose-6-phosphate isomerase (5.3.1.9)	D	TRIS–GLY
GPI-B1,2	Pgi-1,2	Glucose-6-phosphate isomerase (5.3.1.9)	D	TRIS–GLY
G3PDH-1	Agp	Glycerol-3-phosphate dehydrogenase (1.1.1.8)	D	TRIS–GLY and CAME6.3
HAGH		Hydroxyacylglutathione hydrolase (3.1.2.6)	D	TRIS–GLY
LDH-A1	Ldh-1	Lactate dehydrogenase (1.1.1.27)	T	TRIS–GLY
sMDH-A1,2	Mdh-1,2	Cytosolic malate dehydrogenase (1.1.1.37)	D	CAME6.3
sMDH-B1,2	Mdh-3,4	Cytosolic malate dehydrogenase (1.1.1.37)	D	CAME6.3
mMEP-1	Me (MDHp-1)	Mitochondrial $NADP^+$-dependent malate dehydrogenase (1.1.1.40)	T	CAME6.3
PEPD-2	Pp (PDPEP-2)	Proline dipeptidase (3.4.13.9)	D	CAME6.3 and TRIS–GLY
PEP-LT	Ll-1	Peptidase (leucyl-tyrosine substrate) (3.4.-.-)	M	TRIS–GLY
PGDH	6-Pg	Phosphogluconate dehydrogenase (1.1.1.44)	D	CAME6.3
PGM-2	Pgm	Phosphoglucomutase (5.4.2.2)	M	TRIS–GLY and CAME6.3

[a]Nomenclature according to AFS standard (Shaklee et al. 1990a).

[b]Locus symbols used in previous publications (e.g. Johnson 1979; McGregor 1983; Beacham et al. 1985a, 1988).

[c]M = monomer; D = dimer; T = tetramer.

[d]CAME6.3 = pH 6.3 citric acid/aminopropylmorpholine buffer (Clayton and Tretiak 1972) containing 0.005 M EDTA in the electrode buffer stock; TRIS–GLY = pH 8.5 Tris/glycine buffer (Holmes and Masters 1970).

[e]Although this enzyme is a dimer, the isozyme expressed in muscle tissue (CK-$A1_2$) exhibits monomeric patterns of variation in salmonids and other teleost fishes (Ferris and Whitt 1978; Utter et al. 1979).

APPENDIX B. Alleles, relative electrophoretic mobilities,[a] and allele pooling conventions for all recognized alleles at 15 systems in pink salmon.

Locus	Northern baseline[b]	Alleles[c]						Buffer(s)
ADA-2		100+	91	108	(105)[d]			CAME6.3
ALAT	No	100	92	113+	(109)			TRIS–GLY
		100	87	111+	(108)			CAME6.3
CK-A1	No	100	66+	[74]				TRIS–GLY
GPI-A		100	91+	108	(87)			TRIS–GLY
GPI-B1,2		100	200	−64	[25]			TRIS–GLY
G3PDH-1		100	77	190+	(160)	(190)	[290]	TRIS–GLY
		−100	−177	−25+	(−55)	(−42)	[25]	CAME6.3
HAGH	No	100	138	58				TRIS–GLY
LDH-A1	No	−100	−250					TRIS–GLY
sMDH-A1,2		100	−32	147				CAME6.3
sMDH-B1,2		100	124+	61+	(64)	(85)	[130]	CAME6.3
mMEP-1		100	123					CAME6.3
PEPD-2		100	120+	80	[110]	[132]		CAME6.3
		100	111+	90	[108]	[115]		TRIS–GLY
PEP-LT	No	100	90	108	80			TRIS–GLY
PGDH		100	94	86				CAME6.3
PGM-2		100	155+	(135)	25	[250]		TRIS–GLY
		−100	−67	(−85)	−132			CAME6.3

[a]Negative numbers indicate cathodal mobility.
[b]Loci not present in the northern baseline, but present in the southern baseline.
[c]Parentheses = allele recognized prior to initiation of the fishery analysis but pooled with the allele of closest mobility to minimize potential scoring errors. Square brackets = allele first recognized during the fishery analysis and pooled with the recognized allele of closest mobility. Plus sign = one or more additional alleles pooled with this allele.
[d]This allele is not distinguishable from the **100* allele on CAME6.3 buffer.

APPENDIX C. Pink salmon stocks represented in the baselines and used in the MLE comparisons of replicates among the laboratories.

Stock group			
Fraser River	Puget Sound	Canada South Coast	Canada North Coast
Fraser R.[a]	Nooksack R.	Wakeman R.	Johnston Cr.
Thompson R.	Skagit R.	Kakweiken R.	Kilbella R.
Bridge R.	Stillaguamish R.	Glendale Cr.	Koeye R.
Seton Cr.	Hamma Hamma R.	Adam R.	Kwatna R.
Harrison R.	Duckabush R.	Quinsam R.	Bella Coola R.
Vedder R.	Dosewallips R.		Kainet Cr.
			Mussel R.
			Kemano R.
			Quaal R.
			Kitimat R.
			Kumealon Cr.
			Skeena R.
			Lakelse R.
			Morice R.
			Babine R.
			Kispiox R.
			Kitwanga R.
			Khutzeymateen R.
			Kwinamass R.
			Iskheenickh R.
			Iknouk R.

[a]Pink salmon spawning in the mainstem of the Fraser River, primarily between Chilliwack and Hope, British Columbia.

Acute and Final Temperature Preferenda as Predictors of Lake St. Clair Fish Catchability

Roy G. Danzmann[1]

The Great Lakes Institute, University of Windsor, Windsor, Ont. N9B 3P4, Canada

Don S. MacLennan

Lake St. Clair Fisheries Assessment Unit, Ontario Ministry of Natural Resources, Tilbury, Ont. N0P 2L0, Canada

Don G. Hector

Chatham Regional Office, Ontario Ministry of Natural Resources, Chatham, Ont. N7M 5J5, Canada

Paul D. N. Hebert[1]

The Great Lakes Institute, University of Windsor, Windsor, Ont. N9B 3P4, Canada

and Jurek Kolasa

Department of Biology, McMaster University, 1280 Main St. West, Hamilton, Ont. L8S 4K1, Canada

Danzmann, R. G., D. S. MacLennan, D. G. Hector, P. D. N. Hebert, and J. Kolasa. 1991. Acute and final temperature preferenda as predictors of Lake St. Clair fish catchability. Can. J. Fish. Aquat. Sci. 48: 1408–1418.

Geographic distributions of major fish species resident in Lake St. Clair, field assessments of their seasonal thermal distributions, and laboratory determinations of their median and maximum final temperature preferenda were compared with their catchability at different temperatures. Fish catchability at various temperatures was estimated (regression analysis) during the fall pound net set survey (1977–88) using number of fish caught per 24-h net set as the dependent variable. Swimming activity was expected to be higher at temperatures closest to the species' preferred temperature, thereby increasing catchability. Maximum final temperature preferendum was the best predictor of observed fish temperature preferences. Geographic distributions and median final temperature preferenda were better predictors than summer or fall seasonal thermal distributions. Acute temperature preferenda were also good predictors of fish catchability at different temperatures. Of the 22 species examined, the catchability of Centrarchidae (five of six species), Catostomidae (two of five species), Clupeidae (one species), Ictaluridae (two species), and Percichthyidae (two species) was greater in warmer water, while the catchability of Amiidae (one species), Cyprinidae (one species), Catostomidae (three of five species), Esocidae (one species), Percidae (two species), and Sciaenidae (one species) increased in colder water. Temperature significantly accounted for differences in catchability among most species (14 of 22).

Les distributions géographiques des principales espèces de poissons résidant dans le lac Ste-Claire, des évaluations sur place de leur distribution thermique saisonnière et des déterminations en laboratoire de leurs préférendums médians et maximums de la température finale ont été comparées avec leur capturabilité à diverses températures. La capturabilité du poisson à diverses températures a été estimée (par analyse de régression) au cours de relevés d'automne faits avec des enclos (1977–88), en utilisant le nombre des poissons capturés par mouillage de 24 h comme variable dépendante. On s'attendait à ce que l'activité de nage soit plus forte à des températures plus près de la température préférée par l'espèce, ce aurait donc dû augmenter la capturabilité. Le préférendum de la température finale maximum était le meilleur paramètre pour la prévision des préférences de température des poissons. Les distributions géographiques et les préférendums de températures finales médianes permettaient de faire de meilleures prévisions que les distributions thermiques saisonnières de l'été ou de l'automne. Les préférendums aigus de température permettaient également de faire de bonne prévisions de la capturabilité du poisson à diverses températures. Des 22 espèces examinées, la capturabilité des centrarchidés (cinq de six espèces) des catostomidés (deux de cinq espèces), des clupéidés (une espèce), des ictaluridés (deux espèces) et des percichthyidés (deux espèces) était supérieure dans l'eau tiède, alors que la capturabilité des amiidés (une espèce), des cyprinidés (une espèce), des catostomidés (trois de cinq espèces), des ésocidés (une espèce), de percidés (deux espèces) et de sciénidés (une espèce) augmentait dans l'eau froide. La température expliquait de façon significative les différences de capturabilité chez la plupart des espèces (14 sur 22).

Received April 27, 1990
Accepted February 20, 1991
(JA555)

Reçu le 27 avril 1990
Accepté le 20 février 1991

[1]Present address: Department of Zoology, University of Guelph, Guelph, Ont. N1G 2W1, Canada.

Temperature preferences can play an important role in limiting the abundance and distribution of fish species. Fry (1947) postulated that each species has a characteristic final thermal preferendum. This final preferendum tends to be close to the upper lethal temperature for many species (Giattina and Garton 1982). Since temperatures fluctuate seasonally in temperate aquatic ecosystems, species will demonstrate temperature preferenda in the wild which are dependent upon seasonal acclimatizations (McCauley et al. 1977; Hokanson 1977). Temperature preference is also influenced by food availability and by predation–competition interactions (Brandt et al. 1980; Crowder et al. 1981; Adams et al. 1982) and can vary with the age of the fish (McCauley and Huggins 1979). It is generally accepted that thermal preferences in fishes reflect species-specific behavioural responses to seasonal temperature gradients that optimize metabolic functions within these gradients (Brett 1971; Crawshaw 1977; Reynolds and Casterlin 1979; Magnuson et al. 1979). Thus, in natural environments, species exhibit preferences for certain thermal distributions dependent upon seasonal acclimatizations (Ferguson 1958). Laboratory studies which determine acute temperature preference after a short exposure to a temperature gradient are, however, considered to be good measures of temperature preferences of the species in the wild (Fry 1947; Cherry et al 1977; McCauley 1977; Jobling 1981; Giattina and Garton 1982).

The axiom that conspecific individuals have similar preferred temperatures regardless of their geographic origin has been supported by many comparative studies on freshwater fishes (Coutant 1977; Cherry et al. 1977; Spotila et al. 1979; Jobling 1981; Wismer and Christie 1987). However, intraspecific geographic differences in the final temperature preferenda of species have been noted. These differences are most prevelant in comparisons between laboratory and field studies and may be largely due to variable acclimatization conditions associated with seasonal samplings (Wismer and Christie 1987). Some variation in final thermal preferenda is expected, since genetic variation will result in genotypes possessing different physiological thermal optima. The intraspecific variation observed in temperature preferenda prompted Jobling (1981) to propose that each species is characterized by a zone of final preferenda which generally spans 4°C (Wismer and Christie 1987). However, even within the broadened context of a "zone" of final preferendum, examples may be found where species display final preferenda spanning more than 10°C (e.g. freshwater drums) (Wismer and Christie 1987).

Since geographic variation in acute temperature preferenda has been observed for several species, we decided to compare the temperature-dependent catchability of major fish species in Lake St. Clair with expected catchabilities of these species based upon their native geographic range and with temperature preferenda previously reported for these species in other parts of their geographic range. Species occurring at more northerly latitudes might be expected to prefer colder water conditions. The catchability of fish found at more northerly latitudes should, therefore, increase as lake temperatures decrease if their activities increase at lower temperatures. Similarly, the catchability of fish found in more southerly latitudes should increase at higher lake temperatures if activity levels and activity are correlated.

Temperature preference and catchability are expected to be correlated, since there is evidence from physiological studies that fish activity increases at the preferred optimal temperature for the species. Activity levels tend to decrease above or below the optimal temperature for the species (Fry 1967; Brett 1970). Catchability is expected, therefore, to be highest at the species' preferred temperature within the lake because the fish will be most active at this temperature. Also, fish are more likely to be found at their preferred temperature, and therefore, catchability should increase because abundance is higher. However, this must be considered an oversimplification, since many other environmental factors can certainly influence fish catchability in addition to temperature.

This study assesses whether temperature is a good predictor of fish catchability for species resident in Lake St. Clair and documents the rank order of catchability for the various species. If temperature preferenda are species specific, then the rank order of Lake St. Clair species thermal distributions should be highly correlated with reported measures of temperature preferenda. Information on temperature preferences is clearly essential to assess the potential impact of future shifts in lake temperature.

Materials and Methods

A ranking of species catchability for the 22 major fish species present in Lake St. Clair was obtained from weighted regression coefficients, using water temperature as an independent variable to predict species catchability (dependent variable). Separate estimates of temperature versus species catchability using catch per unit effort (CUE, defined as the number of fish caught per 24-h net set) data were obtained at each of four sampling sites in Lake St. Clair and were weighted according to the relative catch of the species at each sampling site (Danzmann et al. 1989). CUE data were geometrically transformed to meet the assumptions of homogeneity of variance. However, outliers were not discarded, since they did not represent sampling error. Rather, outliers were windsorized (z-score scaled to the highest z-score that was not an outlier), and CUEs for each species were then reanalyzed (Sokal and Rohlf 1981). This type of analysis removes the biases that may be inherent in using the present sampling gear because of the differential catchability among the species that may result from using a trap net. By standardizing catches to unit variance, this bias is removed.

Weighted regression coefficients were used to more accurately interpret species abundance at different sampling temperatures lake wide. As an example, consider the difference in the interpretation of results which would result from the following two scenarios (i.e. if species catchability was calculated lake wide or determined by weighting CUEs at each sampling site). In the first case, suppose a species was equally represented at all four sampling sites and was more active when temperatures were warmer. Regardless of whether CUE data were analyzed lake wide or weighted by site, the same conclusion would be reached (i.e. species abundance increases at higher temperatures). In the second scenario, suppose the species was only common at one site (a shallow, warmwater bay, for example) and rare at the other sites. However, within this bay, activity levels and catchability increased as temperatures decreased. A lakewide survey comparing species catchability with temperature would erroneously conclude that catchability of this species and temperature were directly related whereas a weighted regression analysis would truly indicate that the species catchability is higher at lower temperatures.

The 22 species were than ranked in order of their preferences for high to low water temperatures on the basis of the magnitude

of the weighted regression coefficient with temperature. The analysis was based upon data collected by Ontario Ministry of Natural Resources personnel at the Lake St. Clair Fisheries Assessment Unit from 1977 to 1988, using offshore trap net sets (see Hector (1985) and Danzmann et al. (1989) for a description of sampling locations and censusing methods).

Geographic Distributions

The expected rank order of temperature preferences in Lake St. Clair fish was based upon two measures of latitudinal variation in their native geographic distributions in North America. First, we determined the approximate northernmost latitudinal limit of each species. Second, we determined the mean latitudinal distribution of each species by averaging the northernmost and southernmost limits of the species range. All the species were compared except for carp, which is not native to North America. Latitudinal limits were obtained from Scott and Crossman (1973). For the first and second analysis, species were ranked equally if they did not differ by more than 1° or 0.5° of latitude, respectively. It was predicted that an inverse relationship should exist between latitudinal distribution and fish catchability at higher temperatures (i.e. species which are caught more often at higher temperatures are expected to have a more southerly latitudinal distribution). A Spearman rank correlation analysis between the weighted regression coefficients of Lake St. Clair species catchability at different temperatures and the (1) northern or (2) mean latitudinal distributions of these species was used to test this prediction.

Temperature Preferences and Thermal Distributions

Expected seasonal thermal distributions for the 22 major fish species in Lake St. Clair were obtained from data examining laboratory final and acute temperature preferenda and the preferred seasonal thermal distributions of fishes from different regions of the Great Lakes as well as different regions of North America (Table 1). The final temperature perferendum represents the temperature selected by a species if exposed to a long-term continuous temperature gradient, while the acute temperature preferendum reflects the short-term preferred temperature conditional upon previous laboratory acclimations or seasonal acclimatizations (Giattina and Garton 1982). Most of this information is compiled in Wismer and Christie (1987), which lists both final and acute temperature preferenda and seasonal thermal distributions. This source reports the findings from a large number of investigations on fish temperature preferences. This compilation and Mathur et al. (1981) were used as the primary reference sources in this study. Specific references to some of the original source work are indicated in Table 1.

Unfortunately, data for many species are not available on acute preferred temperatures at different acclimation temperatures. Therefore, two comparisons were made with previously published results. The first compared species temperature rankings in Lake St. Clair fishes with their expected final maximum and median temperature preferenda, while the second compared rankings with expected acute preferred temperatures between 10 and 17°C. This range represents water temperatures encountered during the autumn index survey. When two or more investigators reported differences in the final laboratory temperature preferendum of a species, the median value from these studies was used, in addition to the maximum final temperature preference.

For the first comparison, Spearman rank correlation coefficients between temperature preferenda and rankings of Lake St. Clair species catchability directly related to lake temperature were calculated. In addition to final maximum and median temperature preferenda, two other indicators of a species' temperature preferences were compared: summer and fall thermal distributions (data given in Table 1). These two variables were generally obtained from field observations, while estimates of final temperature preferenda are obtained from laboratory studies.

The second comparison was only possible for selected species, since data were not available for acute temperature preferences in all species. For this analysis, expected acute temperature preferences in the acclimation range of 10–17°C were clustered using a single linkage algorithm (Hartigan 1975) and compared with the Lake St. Clair species temperature rankings. Major branch points in the dendrogram were taken to delineate major groupings which were expected to correspond to the temperature rank orderings.

In data summarized by Wismer and Christie (1987) and Mathur et al. (1981), information was available on acute temperature preferences for nine species: common carp, brown bullhead, channel catfish, white perch, rock bass, pumpkinseed, bluegill, smallmouth bass, and yellow perch. Polynomial regression equations generated from the data tabulated in Wismer and Christie (1987) and the regression equations in Mathur et al. (1981) are given in Table 2 and were used to generate the expected acute preferred temperatures for these species. The average acute temperature preference was used to generate the single linkage clustering when more than one source was cited for each species.

Results

Temperature accounts for differences in catchability for 14 of the 22 species examined in Lake St. Clair. However, the maximum amount of variation in catchability for any one species, explained by temperature, is only 6% (Table 3). On a family basis, five of six species belonging to the family Centrarchidae and five species belonging to the families Ictaluridae, Percichthyidae, and Clupeidae all show strong preferences for higher temperatures lake wide. Fish belonging to the families Percidae, Sciaenidae, Esocidae, Amiidae, and Cyprinidae and three of five species belonging to the family Catostomidae appear to prefer cooler water temperatures.

Comparisons with Geographic Distributions

Both the most northern latitude of the species range ($r_s = -0.406$; $N = 21$; $P < 0.05$) and the mean latitude of the species range ($r_s = -0.405$; $N = 21$; $P < 0.05$) were good predictors of Lake St. Clair fish species catchability at different temperatures (Fig. 1 and 2). Species which appeared to prefer warmer water temperatures as exemplified by having native distributions that were more southerly tended to have higher catchabilities at warmer water temperatures. However, exceptions to this general trend were also observed. For example, by dividing the catchability distributions in half with respect to either latitude or temperature, it can be stated that catchability of quillback and silver redhorse sucker increased in warmer water, even though these two species have a fairly northern distribution (Fig. 1 and 2). Conversely, the catchability of bowfin and golden redhorse sucker is fairly low at high temperature,

TABLE 1. Preferred seasonal temperatures of fish species that occur in Lake St. Clair.

Species	Preferred temperature (°C)[a]	Location	Reference
Bowfin (BO), *Amia calva*	30.5 (FP)	Lab	Houston 1982
Gizzard shad (GS), *Dorosoma cepedianum*	10–22 (fa)	Ohio R.	Yoder and Gammon 1976
	20.5 (fa)	Lab	Reutter and Herdendorf 1976
	4–10 (wi)	Ohio R.	Yoder and Gammon 1976
	28.5–31 (su)	Lab	Yoder and Gammon 1976
	26–34 (su)	Ohio R.	Yoder and Gammon 1976
	26–34 (su)	Nanticoke GS	Ellis 1984
	19.0 (su)	Lab	Reutter and Herdendorf 1976
	22.5–23.0 (su)	Tennessee	Dendy 1948
Northern pike (NP), *Esox lucius*	19–20 (FP)	Lab	Casselman 1978
Quillback (QB), *Carpoides cyprinus*	22.1 (fa)	Lab	Reutter and Herdendorf 1974[c]
	10–16 (wi)	Ohio R.	Yoder and Gammon 1976
	26–32 (su)	Ohio R.	Yoder and Gammon 1976
White sucker (CWS), *Catostomus commersoni*	16–19 (fa)	Ohio R.	Yoder and Gammon 1976
	22.4 (fa)	Lab	Reutter and Herdendorf 1974[c]
	14.1–18.3		Brown 1974
	23.9 (sp)		Brown 1974
	25–27 (su)	Ohio R.	Yoder and Gammon 1976
	20.6 (su)	Wisconsin lakes	Hile and Juday 1941
	18.3 (su)	Maine	Cooper and Fuller 1945[c]
	18.9–21.1 (su)	Colorado	Horak and Tanner 1964[c]
	18.3–26.7 (FP)		Wismer and Christie 1987
Silver redhorse (SiRS), *Moxostoma anisurum*	NA		
Golden redhorse (GRS), *Moxostoma erythrurum*	NA		
Shorthead redhorse (ShRS), *Moxostoma macrolepidotum*	26–27.5 (FP)		Yoder and Gammon 1976
Common carp (C), *Cyprinus carpio*	AcThPr[b]		Spotila et al. 1979 (1)
	16–20 (fa)	Ohio R.	Yoder and Gammon 1976
	5–16 (wi)	Ohio R.	Yoder and Gammon 1976
	27.4 (sp)	Lab	Spotila et al. 1979
	29.7 (su)	Lab	Spotila et al. 1979
	26–34 (su)	Ohio R.	Yoder and Gammon 1976
	29–32 (FP)		Jobling 1981
	29.3–31.9 (FP)		Wismer and Christie 1987
	28.2–31.9 (FP)		Coutant 1977
Brown bullhead (BB), *Ictalurus nebulosus*	AcThPr[b]		Richards and Ibara 1978 (1)
	AcThPr[b]		Mathur et al. 1981 (2)
	23.6 (fa)	Lab	Reutter and Herdendorf 1974[c]
	11.9 (wi)	Lab	Reutter and Herdendorf 1974[c]
	10.9 (wi)	Lab	Reutter and Herdendorf 1976
	23.5 (sp)	Lab	Reutter and Herdendorf 1974[c]
	22.4 (sp)	Lab	Reutter and Herdendorf 1976
	27.3–31 (FP)	Lab	Jobling 1981
	29–31 (FP)		Wismer and Christie 1987
Channel catfish (CC), *Ictalurus punctatus*	AcThPr[b]		Spotila et al. 1979 (1)
	AcThPr[b]		Mathur et al. 1981 (2)
	25.3 (fa)	Lab	Reutter and Herdendorf 1974[c]
	25.2 (su)	Lab	Reutter and Herdendorf 1974[c]
	23.0–32.5 (FP)		Wismer and Christie 1987
White perch (WP), *Morone americana*	AcThPr[b]	Lab, North Carolina	Hall et al. 1978 (1)
	AcThPr[b]	Lab, Maryland	Hall et al. 1978 (1)
	AcThPr[b]	Lab, New Jersey	Hall et al. 1978 (1)
	13–19 (wi)[d]	Lab	Talmage 1978
	29–32 (su)[d]		Talmage and Coutant 1979
	21–27 (sp/su)[d]	Connecticut R.	Marcy 1976

TABLE 1. (*Continued*)

Species	Preferred temperature (°C)[a]	Location	Reference
White bass (WB), *Morone chrysops*	16–17 (fa)	Lab	Barans and Tubb 1973[c]
	12–17 (wi)	Lab	Barans and Tubb 1973[c]
	12–17 (sp)	Lab	Barans and Tubb 1973[c]
	28–30 (su)	Lab	Barans and Tubb 1973[c]
	30–34 (su)	L. Erie	Brown 1974
	27.8 (su)	Lab	Reutter and Herdendorf 1976
	29.0–34.4 (FP)		Wismer and Christie 1987
Rock bass (RB), *Ambloplites rupestris*	AcThPr[b]		Cherry et al. 1977 (1)
	22.8 (fa)	Lab	Reutter and Herdendorf 1974[c]
	21.6 (wi)	Lab	Reutter and Herdenford 1974[c]
	20.5 (sp)	Lab	Reutter and Herdendorf 1974[c]
	19.6 (sp)	Lab	Reutter and Herdendorf 1976
	20.2 (su)		Reutter and Herdendorf 1976
	18.7 (su)		Spotila et al. 1979
	14.7–21.3 (su)	Wisconsin lakes	Hile and Judy 1941
	21–30 (FP)		Wismer and Christie 1987
Pumpkinseed sunfish (P), *Lepomis gibbosus*	AcThPr[b]		Evans 1977 (1)
	AcThPr[b]		Mathur et al. 1981 (2)
	28.5 (wi)	Lab	Talmage and Coutant 1979
	31.7 (sp)	Lab	Talmage and Coutant 1979
	24.2 (sp)	Lab	Reutter and Herdendorf 1974[c]
	31.7 (su)	Lab	Talmage and Coutant 1979
	27.7 (su)	Lab	Reutter and Herdendorf 1974[c]
	26.0–31.5 (FP)		Jobling 1981
	26–32 (FP)		Wismer and Christie 1987
Bluegill sunfish (BG), *Lepomis macrochirus*	AcThPr[b]		Carlander 1977
	AcThPr[b]		Brown 1974
	AcThPr[b]		Cherry et al. 1975[e] (1)
	AcThPr[b]		Cherry et al. 1977[e] (1)
	AcThPr[b]		Cravens 1982 (1)
	AcThPr[b]		Mathur et al. 1981 (2)
	19.0 (fa)	Ohio R.	Yoder and Gammon 1976
	30.9–32.3 (FP)		Jobling 1981
	24.6–32.0 (FP)		Wismer and Christie 1987
Smallmouth bass (SB), *Micropterus dolomieui*	AcThPr[b]		Cherry et al. 1977 (1)
	AcThPr[b]		Mathur et al. 1981 (2)
	21–23 (fa)	Lab	Barans and Tubb 1973[c]
	26.6 (fa)	Lab	Cherry et al. 1977
	12–13 (wi)	Lab	Barans and Tubb 1973[c]
	15–16 (sp)	Lab	Barans and Tubb 1973[c]
	30 (su)	Lab	Barans and Tubb 1973[c]
	20.3–21.3 (su)	Wisconsin	Hile and Juday 1941
	21.4 (su)	S. Ontario	Ferguson 1958
	30–31 (su)	Tennessee	Wrenn 1980
	21.3–31.3 (FP)		Coutant 1977
Largemouth bass (LB), *Micropterus salmoides*	AcThPr[b]		Mathur et al. 1981 (2)
	28.5–32 (FP)		Jobling 1981
	26.6–32 (FP)		Wismer and Christie 1987
Black crappie (BC), *Pomoxis nigromaculatus*	24.6 (fa)	Lab	Reutter and Herdendorf 1976
	22.2 (fa)	Lab	Reutter and Herdendorf 1974[c]
	20.7 (wi)	Lab	Reutter and Herdendorf 1976
	20.5 (wi)	Lab	Reutter and Herdendorf 1974[c]
	21.0 (sp)	Lab	Reutter and Herdendorf 1974[c]
	21.7 (su)	Lab	Reutter and Herdendorf 1974[c]
	27.8–29.8 (FP)		Wismer and Christie 1987
	24.0–29.8 (FP)		Coutant 1977
Yellow perch (YP), *Perca flavescens*	AcThPr[b] (fa)		EPA 1976 (1)
	AcThPr[b] (fa)		Mathur et al. 1981 (2)
	AcThPr[b] (fa)		Ferguson 1958 (3)
	AcThPr[b] (juveniles)		Cherry et al. 1977
	AcThPr[b] (wi)		Cravens et al. 1983
	19.7–21.2 (su)	Ontario lakes	Ferguson 1958
	20.2–21.0 (su)	Wisconsin lakes	Hile and Juday 1941
	20.1–23.0 (FP)		Jobling 1981
	18.0–21.1 (FP)		Wismer and Christie, 1987

TABLE 1. (*Concluded*)

Species	Preferred temperature (°C)[a]	Location	Reference
Walleye (W), *Stizostedion vitreum*	20.6–23.2 (FP)	Field	Houston 1982
Freshwater drum (FD), *Aplodinotus grunniens*	19.6 (fa)	Lab	Reutter and Herdendorf 1974[c]
	22–30 (fa)	Ohio R.	Yoder and Gammon 1976
	6–11 (wi)	Ohio R.	Yoder and Gammon 1976
	20–28 (su)	Nebraska	Cada and Hergenrader 1980
	26.5 (su)	Lab	Reutter and Herdendorf 1974[c]
	21.6–22.2 (su)	Tennessee	Dendy 1948
	21.1–31.0 (FP)		Wismer and Christie 1987

[a]Temperature ranges indicated are from data compiled by Wismer and Christie (1987). Not all the sources listed by these authors are indicated. Instead, the preferred temperatures listed were chosen if seasonal acclimations were indicated. (su = summer, wi = winter, sp = spring, fa = fall, ? = season unknown). The range of final temperature preferenda (FP) for each species is indicated. Sources for the data are listed in the appropriate literature review cited. The tabulated preferred temperatures are based upon studies using adults or large fish for all species except white perch. NA = no data available.

[b]Acute thermal preferences (AcThPr) based upon laboratory studies are given in Table 2. Numbers in parentheses indicate the source data for the regression equations given in Table 2.

[c]Cited in Coutant (1977).

[d]Larval preferred temperatures are indicated.

[e]Cited in Mathur and Silver (1980).

TABLE 2. Polynomial regression equations relating acclimatization temperature to acute thermal preferences.

Species	Constant		Partial regression coefficients[a]	R^2
C	26.3925	+	$7.4075x - 0.3968x^2 + 0.0101x^3 - 0.0001x^4$ (1)	0.985
BB	16.6010	−	$1.4921x + 0.1536x^2 - 0.0031x^3$ (1)	0.979
	9.4600	+	$0.8004x$	0.590
CC	−18.0910	+	$13.7895x - 1.8453x^2 + 0.1135x^3 - 0.0032x^4 + 0.000033x^5$ (1)	0.990
	18.8300	+	$0.5870x - 0.0280$bl[c] (2)	0.800
WP	13.9390	+	$0.2527x + 0.2910x^2 - 0.0006x^3$ (1)	0.954
RB[b]	−6.4384	+	$1.6820x + 0.0017x^2 - 0.0006x^3$ (1)	0.950
P	16.79	+	$0.9308x - 0.0167x^2$ (spring)	0.999
	20.90	+	$0.3904x$ (summer) (1)[d]	0.977
	16.43	+	$1.0112x - 0.0240x^2$ (winter) (1)[d]	0.993
	12.35	+	$0.6320x$ (2)	0.560
BG	29.288	−	$3.8475x + 0.4351x^2 - 0.0158x^3 + 0.0002x^4$ (1)	0.975
	15.74	+	$0.5090x$ (2)	0.660
SB	23.39	+	$0.4620x - 0.061$bl[c] (2)	0.790
LB	13.87	+	$0.5870x$ (2)	0.720
YP	9.85	+	$0.9020x - 0.010x^2$ (fall: high temp. preference) (1)[e]	0.965
	7.625	+	$0.9850x - 0.027x^2$ (fall: low temp. preference) (1)[e]	0.793
	7.3374	−	$0.2128x + 0.0483x^2$ (winter)	0.924
	17.86	+	$0.4100x$ (2)	0.310
	−2.8334	+	$3.6279x - 0.1963x^2 + 0.0036x^3$ (3)	0.996

[a]Numbers in parentheses refer to sources listed in Table 1. See Table for species abbreviations.

[b]Data calculated for juveniles.

[c]bl = body length. For the calculation of preferred temperatures for SB and CC from Mathur et al. (1981), maximum bl of 184 and 252 mm, respectively, were used.

[d]Expected acute temperature preferenda calculated by averaging values generated for the winter and summer data.

[e]Expected acute temperature preferrenda calculated by averaging values generated from the high and low temperature data.

TABLE 3. Expected mean summer and fall thermal distribution and expected final temperature preferrenda for major fish species in Lake St. Clair, and a comparison with observed species catchability at different temperatures for species assessed during the fall pound net survey from 1977 to 1988.

Weighted partial regression coefficient species[a] with temperature			Preferred temperature (°C)[c]		Mean thermal distribution (°C)[c]	
		R^2 [b]	Median	Maximum	Fall	Summer
BG	0.131	0.056***	28.3	32.3	19.0	NA
QB	0.106	0.035***	NA	32.0[d]	22.1	29.0
BC	0.104	0.062***	26.9	29.8	23.4	21.7
P	0.099	0.032***	29.0	32.0	NA	29.7
SiRS	0.096	0.030***	NA	NA	NA	NA
CC	0.082	0.031***	27.8	32.5	25.3	25.2
LB	0.071	0.034***	29.3	32.0	NA	NA
WB	0.069	0.016*	31.7	34.4	16.5	29.6
WP	0.063	0.020**	NA	32.0[d]	NA	27.3
GS	0.054	0.028***	NA	31.0[d]	18.3	26.3
BB	0.036	0.005	29.2	31.0	23.6	NA
SB	0.029	0.014*	26.3	31.3	24.3	25.7
FD	0.017	0.000	26.0	31	22.8	24.1
W	0.010	0.006	21.9	23.2	NA	NA
GRS	0.008	0.000	NA	NA	NA	NA
BO	0.007	0.002	30.5	30.5	NA	NA
CWS	0.007	0.004	22.5	26.7	20.0	21.2
RB	−0.021	0.000	25.5	30.0	22.8	19.0
YP	−0.021	0.003	20.5	23.0	NA	20.5
ShRS	−0.044	0.034***	26.8	27.5	NA	NA
C	−0.075	0.051***	30.1	31.9	18.0	29.9
NP	−0.093	0.044***	19.5	20.0	NA	NA

[a]See table 1 for source and species abbreviations.

[b]The coefficient of determination was determined from the catchability of fish at different temperatures lake wide. Regression significant at the *0.05, **0.01, and ***0.001 level, respectively).

[c]NA = no data available.

[d]Maximum final thermal preferendum taken from maximum summer thermal distribution.

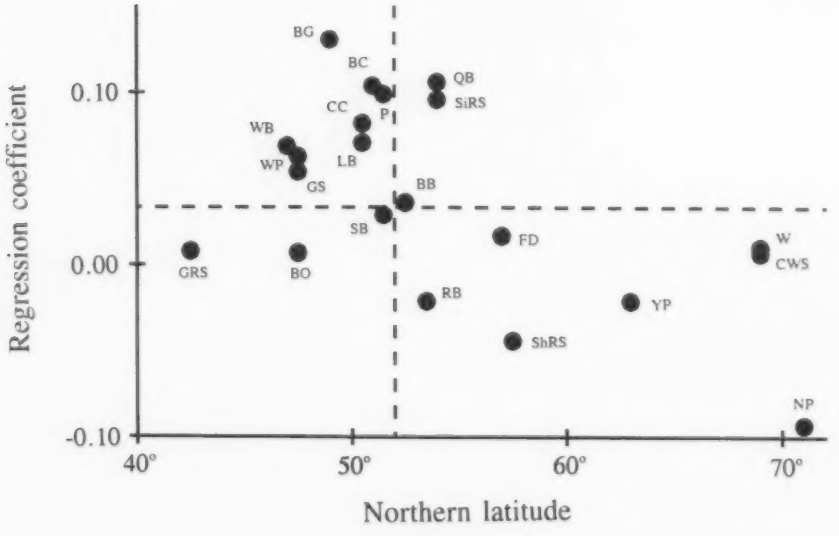


FIG. 1. Association between the catchability of different species in Lake St. Clair with increasing lake temperature (regression coefficients taken from Table 3) and their northernmost latitudinal distribution. Broken lines divide both distributions approximately in half. Species abbreviations are given in Table 1.

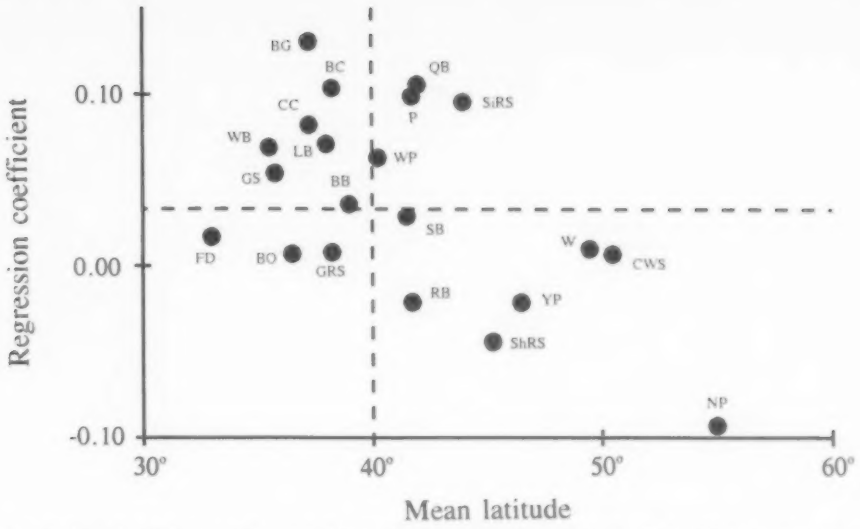


FIG. 2. Association between the catchability of different species in Lake St. Clair with increasing lake temperature (regression coefficients taken from Table 3) and their midlatitudinal distribution (see text for explanation). Broken lines divide both distributions approximately in half. Species abbreviations are given in Table 1.

even though these two species have a more southerly distribution (Fig. 1 and 2). Anomolous associations with pumpkinseed and freshwater drum were observed dependent upon whether the species were ranked according to their northernmost distribution or their mean latitudinal distribution.

Comparisons with Summer and Fall Thermal Distributions

The congruence between observed thermal distributions for Lake St. Clair fishes and the rankings obtained from the summer ($r_s = 0.327$; $N = 13$; $P > 0.10$) and fall ($r_s = 0.077$; $N = 12$; $P > 0.10$) thermal distributions for these species in other parts of their geographic range is poor. Although summer thermal distributions appeared to give a better estimate of species temperature distributions than did reported fall thermal distributions, the associations were not significant (Table 3).

Comparisons with Final Maximum and Median Temperature Preferenda

Final temperature preferenda calculated from laboratory studies gave the best congruence with observed thermal distributions in Lake St. Clair fishes. Maximum final preferred temperatures were better indicators ($r_s = 0.645$, $N = 17$; $P < 0.01$) than were median preferred temperatures ($r_s = 0.411$; $N = 17$; $P < 0.10$). Estimates of final temperature preferenda were not available for quillback, white perch, and gizzard shad. However, if the observed maximum summer thermal distributions are included as an estimate of the maximum final preferred temperature for these three species, the congruence between observed and expected ordinations is increased ($r_s = 0.701$; $N = 20$; $P < 0.01$) (Table 3). However, three species demonstrated exceptions to this general pattern. Bowfin, carp, and rock bass have been reported to have higher final maximum temperature preferenda than the relative rankings of these species for temperature comparisons within Lake St. Clair would indicate (Table 3).

Comparisons with Acute Temperature Preferenda for Selected Species

The single linkage clustering of temperature preferenda for the 10 species revealed four major groupings (Fig. 3). These range from the rock bass which prefers the coolest water temperatures to bluegill, pumpkinseed, and carp which prefer the warmest water temperatures. Largemouth bass, white perch, and channel catfish are also identified as preferring warmer water temperatures than yellow perch, smallmouth bass, and brown bullhead (Fig. 3). The only inconsistencies between expected preferred water temperatures for these species and their relative rankings based upon thermal distributions in Lake St. Clair are for carp.

Discussion

The congruence between the rankings of observed catchability at different temperatures of fish species in Lake St. Clair and both the acute preferred temperatures and final maximum temperature preferenda is remarkable. Similar conclusions were reached in comparisons of fish abundance in thermal discharge from electric generating plants with their final laboratory temperature preferenda (Clugston 1973; Coutant 1975; Stauffer et al. 1975). These findings provide further support for the conclusion that final temperature preferenda are fairly stable over wide geographic ranges (Beitinger and Fitzpatrick 1979; Reynolds and Casterlin 1979) and are good predictors of a species' distribution across a range of environmental temperatures.

In the absence of detailed information on a species' final temperature preferendum, knowledge of the geographic distribution of a species appears to provide reliable information on expected field temperature distributions. However, major deviations from expected distributions may be observed (e.g. quillback, silver redhorse sucker, golden redhorse sucker, and bowfin in the present study) that may only be explainable by

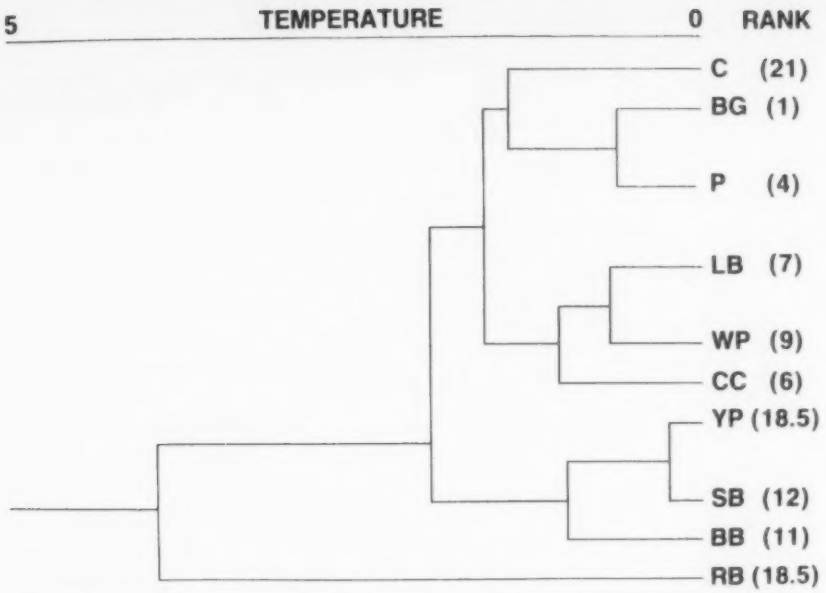


FIG. 3. Single linkage hierarchical clustering of species acute temperature preferences in an acclimation temperature range of 10–17°C. Rankings correspond to ordinations of species temperature preferences (Table 3) in Lake St. Clair. Species abbreviations are given in Table 1.

more detailed studies of behavioural differences between species or laboratory studies determining final temperature preferenda.

Observations on seasonal temperature preferences are relatively poor predictors of species temperature preferences because estimates represent a narrower range of short-term selected temperatures. Seasonally selected temperatures do not necessarily reflect the optimum range for physiological functions and may be conditional upon immediate environmental variables such as food resources, habitat type, predation, or competition (Keast 1978).

Three species (carp, bowfin, and rock bass) were found in cooler water in Lake St. Clair than might be expected on the basis of past analyses. Houston (1982) and Spotila et al. (1979) reported that summer temperature preferences were higher than 28°C in carp and bowfin. Behavioural differences displayed by carp and bowfin may account for the differences between data sets. Normally, these species are found in shallow, weedy, inshore areas of the lake where water temperatures are higher than average compared with adjacent open-water areas of the lake. Carp and bowfin may remain in these areas until late in the fall when inshore waters experience a rapid cooling because of sustained cooler air temperatures. At this point in time, these species may migrate in larger numbers than usual to deeper parts of the lake that are warmer (L. Laforet, pers. comm.). Since lake temperatures steadily decline during the censusing period in autumn, the majority of these fish are probably caught in the trap nets towards the latter part of the season as they migrate into deeper, warmer water.

Observed summer–fall temperature preferenda in rock bass determined from laboratory and field observations were much lower than estimated final temperature preferences in the species (Table 1). Studies on temperature preferenda generally indicate higher temperature preferences in laboratory-reared fish compared with field-acclimatized conspecifics (Ferguson 1958). An examination of the data presented in Table 1 certainly substantiates this general conclusion, as mean summer preferred temperatures tended to be lower than median final preferred temperatures for all species except pumpkinseed and yellow perch, in which field and laboratory observations gave very similar results.

For most species, reports of mean summer preferred temperatures are no lower than 10% of the reported final median preferred temperature. However, for rock bass and black crappie, reported summer preferred temperatures were 26 and 13% lower, respectively, than median estimates of final preferred temperatures. Also, final temperature preferenda were reported to span 9°C in rock bass (Wismer and Christie 1987). Such wide variation in final temperature preferences for adult members of a species is unusual and was only observed in three other species: channel catfish, smallmouth bass, and freshwater drum. The reason for such wide variation in final temperature preferenda in these species is unknown but may relate to differences in the genetic background of the various stocks used in the determination of final temperature preferenda.

Differences in observed temperature preferenda within a species may result because conspecific populations differ in their genetic backgrounds and consequent physiological preferences for different temperatures. As a test of this hypothesis, Koppelman et al. (1988) compared four stocks of largemouth bass belonging to two subspecies. Final temperature preferenda were very similar among all four stocks despite a large degree of genetic differentiation. These results suggest that even when quite substantial genetic differentiation exists among fish stocks, final thermal preferenda are likely to be species specific and thus comparable across wide geographic distances. However, it is interesting to note that the F_1 hybrids between these southern and northern subspecies of largemouth bass had higher critical thermal maxima than their maternal subspecies at all temperatures tested (Fields et al. 1987). The possibility that

TABLE 4. Comparison of species assemblages which are expected to show avoidance responses to summer water temperatures greater than 28°C and those which are expected to be unaffected.[a]

Species preferring water temp. less than 28°C	Species tolerating water temp. greater than 28°C[c]
NP	BO?
CWS	GS
GRS	SiRS
ShRS	QB
BB[b]	C?
RB[b]	CC
FD[b]	WP
SB[b]	WB
BC[b]	P
YP	BG
W	LB

[a]Based upon data compiled in Wismer and Christie (1987) and data from the present study.

[b]Seasonal acclimation studies indicate temperature preferences less than 28°C, but laboratory studies indicate that final temperature preferences may exceed 28°C.

[c]A question mark means that laboratory studies indicate a temperature preference exceeding 28°C, but catchability studies from Lake St. Clair indicate a lower thermal distribution for these species.

more definitive differences correlated with genetic distances and average heterozygosities may be evident when estimates of critical thermal maxima are used instead of final temperature preferenda awaits further testing.

Based upon the data compiled by Wismer and Christie (1987) and results from the present study, it is possible to group the 22 major species resident in Lake St. Clair into species assemblages that may be differentially influenced by future water temperature increases. At present, summer water temperatures rarely exceed 27°C in Lake St. Clair. Therefore, it was considered of interest to examine the preferred summer water temperatures of the species resident in the lake and arbitrarily divide these species into two groups: one group (11 species) whose summer temperature preferenda may be above 28°C and another group (11 species) which appears to prefer cooler summer water temperatures based upon field observations (Table 4). For five of the 11 species in the latter group, laboratory studies indicate that maximum preferred temperatures may exceed 28°C. Although no temperature preferences for silver redhorse and golden redhorse sucker have been reported, it is also possible to assign these two species to a group by virtue of their observed temperature preferences in Lake St. Clair. It is expected that silver redhorse sucker will tolerate temperatures exceeding 28°C, while golden redhorse sucker will prefer cooler temperatures.

A temperature of 28°C was considered most informative, as future lakewide temperatures may reach this plateau in successive years, if global warming trends increase. Changes in future mean summer water temperatures should be reflected by changes in species abundance for the two major groupings listed in Table 4. Such changes may impact adversely on the economically important sportfishing industry in Lake St. Clair by reducing favourable habitat conditions for the walleye which is the major sport fish in Lake St. Clair and the second most abundant fish species in the lake after the freshwater drum. However, in the southern United States, walleye fishing is quite popular in lakes and man-made reservoirs where summer water temperatures may be quite high. This suggests that within this species there may be several genetic stocks or clones that can withstand greater extremes in temperature. The wide range in reported seasonal preferred temperatures in walleye and northern pike and species showing a wider range in temperature preferences such as the brown bullhead, rock bass, and freshwater drum (Table 4) suggest that certain species have broader seasonal temperature preferences which may result from genetic differences between stocks even though final temperature preferenda may remain fairly constant or species specific.

Acknowledgements

Special thanks are extended to Larry Laforet, Stan Powell, Rob MacDonald, and other members of the Ontario Ministry of Natural Resources Lake St. Clair Fisheries Assessment Unit survey crews who helped collect the fall census data on Lake St. Clair fishes from 1977 to 1988. We also wish to thank Dr. Ed Crossman for his interest in the study and for bringing to our attention the temperature data compilations on Great Lakes fishes by Wismer and Christie. The helpful comments by Drs. Bill Beamish and John Kelso on earlier versions of this manuscript are appreciated. This work was supported by the Ontario Ministry of Natural Resources through the Renewable Resources Research Grant Program.

References

ADAMS, S. M., R. B. MCLEAN, AND M. M. HUFFMAN. 1982. Structuring of a predator population through temperature-mediated effects on prey availability. Can. J. Fish. Aquat. Sci. 39: 1175–1184.

BARANS, C. A., AND R. A. TUBB. 1973. Temperatures selected seasonally by four fishes from western Lake Erie. J. Fish. Res. Board Can. 30: 1697–1703.

BEITINGER, T. L., AND L. C. FITZPATRICK. 1979. Physiological and ecological correlates of preferred temperature in fish. Am. Zool. 19: 319–329.

BRANDT, S. B., J. J. MAGNUSON, AND L. B. CROWDER. 1980. Thermal habitat partitioning by fishes in Lake Michigan. Trans. Am. Fish. Soc. 190: 469–478.

BRETT, J. R. 1970. Fishes, functional responses, p. 515–560. *In* O. Kinne [ed.] Marine ecology. Vol. I. Environmental factors. Wiley-Interscience, New York, NY.

1971. Energetic responses of salmon to temperature: a study of some thermal relations in the physiology and freshwater ecology of sockeye salmon (*Oncorhynchus nerka*). Am. Zool. 11: 99–113.

BROWN, H. W. 1974. Handbook of the effects of temperature on some North American fishes. American Electric Power Service Corp., Canton, OH. 524 p.

CADA, G. F., AND G. L. HERGENRADER. 1980. Natural mortality rates of freshwater drum larvae in the Missouri River. Trans. Am. Fish. Soc. 109: 479–483.

CARLANDER, K. E. 1977. Handbook of freshwater fishery biology. Vol. 2. Iowa State University Press, Ames, IA. 431 p.

CASSELMAN, J. M. 1978. Effects of environmental factors on growth, survival, activity, and exploitation of northern pike. Am. Fish. Soc. Spec. Publ. 11: 114–128.

CHERRY, D. S., K. L. DICKSON, AND J. CAIRNS, JR. 1975. Temperatures selected and avoided by fish at various acclimation temperatures. J. Fish. Res. Board Can. 32: 485–491.

CHERRY, D. S., K. L. DICKSON, J. CAIRNS, JR., AND J. R. STAUFFER. 1977. Preferred, avoided, and lethal temperatures of fish during rising temperature conditions. J. Fish. Res. Board Can. 34: 239–246.

CLUGSTON, J. P. 1973. The effects of heated effluents from a nuclear reactor on species diversity, abundance, reproduction and movement o fish. Ph.D. thesis, University of Georgia, Athens, GA. 104 p.

COOPER, G. P., AND J. L. FULLER. 1945. A biological survey of Moosehead Lake and Haymock Lake, Maine. Maine Dep. Inland Fish Game Fish Serv. Rep. 6: 160 p.

COUTANT, C. C. 1975. Temperature selection by fish: a factor in powerplant impact assessments, p. 575–597. *In* Environmental effects of cooling systems at nuclear power plants. International Atomic Energy Agency (IAEA), Vienna.

1977. Compilation of temperature preference data. J. Fish. Res. Board Can. 34: 739–745.

CRAVENS, J. B. 1982. Thermal effects. J. Water Pollut. Control Fed. 54: 812–829.

CRAVENS, J. B., M. E. HARRELSON, AND S. S. TALMAGE. 1983. Thermal effects. J. Water Pollut. Control Fed. 55: 787–800.

CRAWSHAW, L. I. 1977. Physiological and behavioral reactions of fishes to temperature change. J. Fish. Res. Board Can. 34: 730–734.

CROWDER, L. B., J. J. MAGNUSON, AND S. B. BRANDT. 1981. Complementarity in the use of food and thermal habitat by Lake Michigan fishes. Can. J. Fish. Aquat. Sci. 38: 662–668.

DANZMANN, R. G., J. KOLASA, AND P. D. N. HEBERT. 1989. Lake St. Clair fishes: an examination of environmental, variables influencing their distribution and abundance from 1977–1988. The Great Lakes Institute Report, University of Windsor, Windsor, Ont. 191 p.

DENDY, J. S. 1948. Predicting depth distribution of fish in three TVA storage-type reservoirs. Trans. Am. Fish. Soc. 75: 65–71.

ELLIS, C. J. 1984. Predicted survival of selected fish species released via fish pump to untempered discharge water at Nanticoke TGS. Environ. Stud. Assess. Dep. Report 84355: 44 p.

EPA. 1976. Yellow perch select unnaturally high temperatures in laboratory gradient tanks, p. 14. *In* Quarterly report of the environmental research laboratory — Duluth, Minn. U.S. EPA, Office of Research and Development, Duluth, MN. 16 p.

EVANS, D. O. 1977. Seasonal changes in standard metabolism, upper and lower thermal tolerance and thermoregulatory behaviour of the pumpkinseed, *Lepomis gibbosus*, Linnaeus. Ph.D. thesis, University of Toronto, Toronto, Ont. 429 p.

FERGUSON, R. G. 1958. The preferred temperature of fish and their midsummer distribution in temperate lakes and streams. J. Fish. Res. Board Can. 15: 607–624.

FIELDS, R., S. S. LOWE, C. KAMINSKI, G. S. WHITT, AND D. P. PHILIPP. 1987. Critical and chronic thermal maxima of northern and Florida largemouth bass and their reciprocal F_1 and F_2 hybrids. Trans. Am. Fish. Soc. 116: 856–863.

FRY, F. E. J. 1947. Effects of the environment on animal activity. Univ. Toronto Stud. Biol. Ser. 55.

1967. Responses of vertebrate poikilotherms to temperature, p. 375–410. *In* A. H. Rose [ed.] Thermobiology. Academic Press, London and New York.

GIATTINA, J. D., AND R. R. GARTON. 1982. Graphical model of thermoregulatory behavior by fishes with a new measure of eurythermality. Can. J. Fish. Aquat. Sci. 39: 524–528.

HALL, L. W. JR., C. H. HOCUTT, AND J. R. STAUFFER, JR. 1978. Implication of geographic location on temperature preference of white perch, *Morone americana*. J. Fish. Res. Board Can. 35: 1464–1468.

HARTIGAN, J. A. 1975. Clustering algorithms. John Wiley and Sons, New York, NY.

HECTOR, D. G. 1985. Fall pound net program: Lake St. Clair, 1985. Ont. Minist. Nat. Resour. Lake St. Clair Fish. Assess. Unit Rep. 1985-5: 52 p.

HILE, R., AND C. JUDAY. 1941. Bathymetric distribution of fish in lakes of the northeastern highlands, Wisconsin. Trans. Wis. Acad. Sci. Arts Lett. 33: 147–187.

HOKANSON, K. E. F. 1977. Temperature requirements of some percids and adaptations to the seasonal temperature cycle. J. Fish. Res. Board Can. 34: 1524–1550.

HORAK, O. L., AND H. A. TANNER. 1964. The use of vertical gill nets in studying fish depth distribution, Horsetooth Reservoir, Colorado. Trans. Am. Fish. Soc. 93: 137–145.

HOUSTON, A. H. 1982. Thermal effects upon fishes. Natl. Res. Counc. Can. Assoc. Comm. Sci. Criteria Environ. Qual., Ottawa, Ont. 200 p.

JOBLING, M. 1981. Temperature tolerance and the final preferendum: rapid methods for the assessment of optimum growth temperatures. J. Fish Biol. 19: 439–455.

KEAST, A. 1978. Trophic and spatial interrelationships in the fish species of an Ontario temperate lake. Environ. Biol. Fishes 3: 7–31.

KOPPELMAN, J. B., G. S. WHITT, AND D. P. PHILIPP. 1988. Thermal preferenda of northern, Florida, and reciprocal F_1 hybrid largemouth bass. Trans. Am. Fish. Soc. 117: 238–244.

MAGNUSON, J. J., L. B. CROWDER, AND P. A. MEDVICK. 1979. Temperature as an ecological resource. Am. Zool. 19: 331–343.

MARCY, B. C. JR. 1976. Fishes of the lower Connecticut River and the effects of the Connecticut Yankee Plant. *In* D. Merrimann and L. M. Thorpe [ed.] The Connecticut River Ecological Study: the impact of a nuclear power plant. Am. Fish. Soc. Monogr. 251 p.

MATHUR, D., R. M. SCHUTSKY, E. J. PURDY, JR., AND C. A. SILVER. 1981. Similarities in acute temperature preferences of freshwater fishes. Trans. Am. Fish. Soc. 110: 1–13.

MATHUR, D., AND C. A. SILVER. 1980. Statistical problems in studies of temperature preference of fishes. Can. J. Fish. Aquat. Sci. 37: 733–737.

MCCAULEY, R. W. 1977. Laboratory methods for determining temperature preference. J. Fish. Res. Board Can. 34: 749–752.

MCCAULEY, R. W., J. R. ELLIOT, AND L. A. READ. 1977. Influence of acclimation temperature on preferred temperature in the rainbow trout, *Salmo gairdneri*. Trans. Am. Fish. Soc. 106: 362–365.

MCCAULEY, R. W., AND N. W. HUGGINS. 1979. Ontogenetic and non-thermal seasonal effects on thermal preferenda of fish. Am. Zool. 19: 267–271.

REUTTER, J. M., AND C. E. HERDENDORF. 1974. Environmental evaluation of a nuclear power plant on Lake Erie. Ohio State Univ. Project F-41-R-5. U.S. Fish Wildl. Serv. Rep. 6/1/73-5/31/74: 84 p.

1976. Thermal discharge from a nuclear power plant: predicted effects on Lake Erie fish. Ohio J. Sci. 76: 39–45.

REYNOLDS, W. W., AND M. E. CASTERLIN. 1979. Behavioral thermoregulation and the "final preferendum" paradigm. Am. Zool. 19: 211–224.

RICHARDS, F. P., AND R. M. IBARA. 1978. The preferred temperatures of the brown bullhead (*Ictalurus nebulosus*) with reference to its orientation to the discharge canal of a nuclear power plant. Trans. Am. Fish. Soc. 107: 288–294.

SCOTT, W. B., AND E. J. CROSSMAN. 1973. Freshwater fishes of Canada. Department of Fisheries and Oceans, Ottawa, Ont.

SPOTILA, J. R., K. M. TERPIN, R. R. KOONS, AND R. L. BENATI. 1979. Temperature requirements of fishes from eastern Lake Erie and the upper Niagara River: a review of the literature. Environ. Biol. Fishes 4: 281–307.

SOKAL, R. R., AND F. J. ROHLF. 1981. Biometry: the principles and practice of statistics in biological research. W. H. Freeman and Company, San Francisco, CA.

STAUFFER, J. R., D. S. CHERRY, K. L. DICKSON, AND J. CAIRNS, JR. 1975. Laboratory and field temperature preference and avoidance data of fish related to the establishment of standards, p. 119–139. *In* S. B. Saila [ed.] Fisheries and energy production: a symposium. Lexington Books, Toronto and London.

TALMAGE, S. S. 1978. Thermal effects on aquatic organisms: an annotated bibliography of the 1976 literature report ORNL/EIS-124. Oak Ridge National Laboratory, Oak Ridge, TN. 249 p.

TALMAGE, S. S., AND C. C. COUTANT. 1979. Thermal effects. J. Water Pollut. Control Fed. 52: 1517–1554.

WISMER, D. A., AND A. E. CHRISTIE. 1987. Temperature relationships of Great Lakes fishes: a data compilation. Great Lakes Fish. Comm. Spec. Publ. No. 87-3: 165 p.

WRENN, W. B. 1980. Effects of elevated temperature on growth and survival of smallmouth bass. Trans. Am. Fish. Soc. 109: 617–625.

YODER, C. O., AND J. R. GAMMON. 1976. Seasonal distribution and abundance of Ohio River fishes at the J. M. Stuart Electric Generating Station, p. 284–295. *In* G. W. Esch and R. W. McFarlane [ed.] Thermal ecology II. Natl. Tech. Info. Serv., Springfield, VA. 404 p.

Abundance and Feeding of Medusae and their Potential Impact as Predators on Other Zooplankton in Bedford Basin (Nova Scotia, Canada) during Spring

Sophie Matsakis

Station Zoologique, BP 28, 06230 Villefranche-sur-Mer, France

Robert J. Conover

Department of Fisheries and Oceans Canada, Bedford Institute of Oceanography, P.O. Box 1006, Dartmouth, N.S. B2Y 4A2, Canada

Matsakis, S., and R. J. Conover. 1991. Abundance and feeding of Medusae and their potential impact as predators on other zooplankton in Bedford Basin (Nova Scotia, Canada) during spring. Can. J. Fish. Aquat. Sci. 48: 1419–1430.

Only five hydromedusan species (*Sarsia princeps, Euphysa tentaculata, Rathkea octopunctata, Cosmetira* sp., and *Aglantha digitale*) and one scyphomedusan (*Aurelia aurita*) were found in the upper 30 m of Bedford Basin during spring 1988. Medusan carbon weight and that of total zooplankton varied reciprocally, suggesting significant population control by gelatinous predators. In March, when zooplankton concentration was low (5–9 mg $C \cdot m^{-3}$) and medusan weight less than 1% of this total, daily ingestion by medusans did not exceed 10% of zooplankton carbon weight. In May, when mesozooplankton concentration was greater than 10 mg $C \cdot m^{-3}$ and predators more abundant, their potential daily impact was at least 59%. From March to June, mean impact was 15.8%. During this period, as medusans increased and copepods decreased, the proportion of copepods consumed continued to increase, while the fraction of eggs consumed, primarily those of potential competitors such as ctenophores and chaetognaths, decreased. Predation between different taxa of medusans was also found. A population decrease in *Rathkea octopunctata*, the dominant spring hydromedusan, may have been attributable to predation by *Aurelia aurita*.

Au printemps 1988, la diversité spécifique des méduses dans les 30 premiers mètres du Bassin de Bedford était faible : seules cinq espèces d'hydroméduses (*Sarsia princeps, Euphysa tentaculata, Rathkea actopunctata, Cosmetira* sp. et *Aglantha digitale*) et une scyphoméduse (*Aurelia aurita*) y ont été dénombrées. La relation négative observée entre le poids des méduses et celle du zooplancton suggère que les prédateurs gélantineux exercent un contrôle significatif sur les populations du bassin. En mars, alors que le poids carbone de zooplancton variait entre 5 à 9 mg $C \cdot m^{-3}$ et que celui des méduses était inférieur à 1 % du total, l'ingestion par les méduses n'a pas excédé 10 % du poids de carbone représenté par le zooplancton. En mai, alors que le poids carbone total était supérieure à 10 mg $C \cdot m^{-3}$, et les prédateurs plus abondants, leur impact potentiel pouvait atteindre au moins 59 %. De mars à juin, l'impact moyen de prédation par les méduses était de 15,8 %. Durant cette période, les méduses sont devenues plus abondantes à mesure que le nombre de copépodes diminuait, et la proportion de copépodes utilisés par les prédateurs augmentait. En même temps, la fraction d'œufs consommés (pour la plupart ceux de compétiteurs potentiels et de copépodes) diminuait. Une prédation interspécifique entre les populations de méduses a été mise en évidence. Elle doit avoir des effets secondaires sur le reste de la communauté zooplanctonique. Ainsi, le déclin de la population de *Rathkea octopunctata* est attribué à la prédation par *Aurelia aurita*.

Received February 20, 1990
Accepted February 20, 1991
(JA482)

Reçu le 20 février 1990
Accepté le 20 février 1991

Medusae are active gelatinous predators and, when moderately abundant, are often a key factor influencing the population dynamics of other zooplankton (Huntley and Hobson 1978; Möller 1980a, 1980b; Grice et al. 1980; Daan 1986). Field observations also suggest that the devastating effects of jellyfish on populations of other zooplankton can facilitate phytoplankton blooms by keeping the populations of grazing herbivores low. However, the seasonal manifestations of this phenomenon and class of cnidarians or ctenophores, presumed to be responsible, vary considerably. Although increased nutrients from agricultural and domestic sources probably contributed to late-summer blooms of dinoflagellates in Gullmar Fjord, Sweden, Lindahl and Hernroth (1983) suggested that reduced grazing pressure following depredations of the scyphomedusan *Aurelia aurita* on populations of herbivorous zooplankton may have been the more important factor. In Kiel Bight, adjacent to the Kattegatt and Skagerrak, with which Gullmar Fjord exchanges, *Aurelia aurita* dominated zooplankton from June to September, accounting for about 50% of the total organic carbon and almost 80% of the dry weight of all mesozooplankton. The decline in crustacean zooplankton concentration in summer apparently leads to a persistent bloom of diatoms, dinoflagellates, and cyanobacteria extending from July through October (Möller 1979). Following the spring bloom in April and May in Saanich Inlet, a fjord on Vancouver Island, large concentrations (>110 mg dry wt·m^{-3}) of the hydro-

medusan *Phialidium gregarium* reduced the herbivore populations sufficiently for a second "spring" bloom to develop in June and July (Huntley and Hobson 1978).

In each of these investigations, the role of jellyfish was surmised from their dominance and correlative changes, but with slopes of opposite sign, in the populations of other animal and plant plankton. Elsewhere, laboratory studies have provided valuable information about swimming behaviour, feeding mechanisms, food selection, and capture rates for different combinations of predator and potential prey (Lebour 1923; Fraser 1969; Mills 1981; Bailey and Batty 1983, 1984; Fulton and Wear 1985; Daan 1986, 1989; Båmstedt 1990), but the application of such experimentally determined rates to estimate predatory impact in the field can be misleading. Because cnidarians generally do not actively hunt specific prey, confining such predators with one or a few prey can lead to unnaturally high encounter rates or false information on feeding preferences (Purcell 1985). The significance of container size in feeding experiments with larval fish and their gelatinous predators has also been emphasized by de Lafontaine and Leggett (1987). Alternatively, the determination of gut contents of preserved animals, along with experimentally measured digestion times, can be used to estimate feeding rates (Möller 1980b; Larson 1987a, 1987b).

Whatever the method used to investigate food-getting in gelatinous predators, the impact on other planktonic populations seems to be greatest when the dominant predator is either a ctenophore (e.g. *Mnemiopsis, Pleurobrachia*) or a scyphomedusan such as *Aurelia aurita*. Even in these groups, daily consumption of their food stock rarely exceeds 50% in the natural environment (Alldredge 1984) but can approach 100% in mesocosms (Harris et al. 1982). The case for enhanced phytoplankton growth through predatory removal of grazers would also seem to be equivocal, the collapse of copepod stocks in the Southern Bight of the North Sea apparently being related to food limitation rather than predation (Daan 1989). On the other hand, there was no relation, positive or negative, between phytoplankton and zooplankton in the North Sea off Northumberland, yet predator control of herbivore grazing would best account for the fall phytoplankton bloom in that area of weak stratification (Roff et al. 1988).

In this paper we ask whether the Hydromedusae can exert a major impact on the zooplankton of a relatively eutrophic environment during the spring when food limitation would not seem to be a serious concern for the grazers. As the method of choice, we have combined maximum rates of predation determined from gut contents and gut-evacuation rates with field data on population abundances to estimate potential predation pressure. The environment chosen was Bedford Basin (Nova Scotia, Canada), a relatively small inlet which has been studied on a frequent, although not routine, basis since 1967. Its physical oceanography and pelagic biology are relatively well known. At this season, the dominant gelatinous predator is the anthomedusan *Rathkea octopunctata* for which there is evidence that it is at least partially responsible for unexpectedly low zooplankton concentrations in spring (Conover and Mayzaud 1975).

Materials and Methods

Study Site

Bedford Basin is a relatively small fjord-like inlet with a maximum depth of about 70 m, a surface area of 17 km^2, and a volume of 5.6×10^8 m^3. Freshwater influx, largely from the Sackville River, varies from 10^4 to 10^7 $m^3 \cdot d^{-1}$ (about 0.002 to 2% of the volume). The basin is separated from open coastal water by a channel of 10 km length and sill depth at its narrowest point (400 m) is about 20 m (Platt and Conover 1971). The spring bloom usually starts in February with peak production in March (>30 mg $C \cdot m^{-3} \cdot h^{-1}$) and with high rates persisting into April, often followed by secondary peaks in May (Conover and Mayzaud 1984). The copepod population develops relatively slowly through May and June, but accelerates to a plateau in excess of 10^5 individuals$\cdot m^{-3}$ (all stages) in July that usually persists through September (Poulet 1978). We know less about the gelatinous predators, but medusans generally predominate in spring, the ctenophore *Pleurobrachia pileus* in fall, while chaetognaths are found all year (Sameoto 1971).

Sampling and Chemical Analysis

To estimate the standing stock of medusans and mesozooplankton, vertical zooplankton tows, from 30 m to the surface, were taken on 15 occasions between March 8 and June 24, 1988, with two different nets towed sequentially, one of 200 μm and 0.75 m in diameter to sample both prey and predators and a second of the same diameter and 800 μm to separate gelatinous predators from their potential prey, thereby reducing contamination of gut contents. All tows were made between 10:00 and 12:00 at the same location near the centre of the basin and immediately preserved in 1% neutral formalin to further reduce the possibility of cod-end feeding. The nets were unmetered, but because of the relatively coarse mesh of both nets and relatively small volume sampled (25 m^3), we assumed a sampling efficiency of 100% for each.

Medusans and other gelatinous predators were counted in all tows before further treatment. Contents of both tows were then split and dry and carbon weight were determined on one half as follows: to separate zooplankton from the contaminating long-chain spring phytoplankton, remembering that the volume filtered for both of the paired tows was assumed to be the same, half of each tow was combined with half of the other and then partitioned by shaking into a 200–800 μm and a >800 μm sample, using a column of screens continuously rinsed with filtered seawater (Hargrave et al. 1985). Each fraction was then dried for 7 d at 60°C, prior to weighing and determination of carbon and nitrogen content using a Perkin Elmer 240 analyser.

The contents of the duplicate half of the coarser two were then processed for gut contents. For medusans, the manubrium was cut longitudinally to release contents which were classified into several categories microscopically. Other gelatinous predators were not numerous, but when noted, their gut contents were also recorded. Prey, primarily copepods and eggs >200 μm, were enumerated in subsamples for the finer net half using a Dollfius cell and a binocular microscope. Representative samples of prey taken from separate tows were also weighed and their carbon and nitrogen contents determined.

To obtain animals in good condition for laboratory studies such as feeding behaviour, digestion time, and also to supply material for chemical analyses, we built a "jelly-fish net" 1 m in diameter with a mesh of 1800 μm and a large codend in the form of a cuboid (25 × 25 × 28 cm with a screened area and attachment collar 12 cm high) of Lexan which could be uncoupled from its supporting frame and then could be used as an observation chamber or to transport experimental material to

the laboratory without further disturbance. For each species, dry weight and elemental composition were determined after immersing living specimens for a few seconds in Bouin's solution to partially fix the animals and to make their manipulation easier (Gorsky et al. 1988), followed by three successive rinses of distilled water to remove excess fixative and sea salt before transferal to tared filters. Dry weight and CHN content were then determined as above. For species which changed size during the period of our observations, i.e. in bell diameter as for *Aurelia aurita* or bell height as in *Aglantha digitale*, the appropriate measurement was made using silouette photographs (Braconnot 1985) of living animals taken shortly after capture, some of which were then processed for chemical analysis as above. The resulting regression equations, giving carbon and nitrogen weight of medusans in relation to bell dimensions, were used in later analysis to estimate chemical composition routinely. For *Rathkea octopunctata*, two sizes were recognized, juveniles and adults, and analysed separately; besides being smaller in size, juveniles also have a less-developed, less-convex umbrella. The remaining hydromedusan species were sufficiently uniform in size to be averaged during determination of weight and chemical composition.

Estimating Digestion Time and Ration

Digestion time was determined, after 24 h of starvation, by first feeding medusans in the laboratory with copepods (200–500 μm length) or eggs from the tows (largely of chaetognaths or ctenophores) or, in feeding *Aurelia aurita*, copepods and eggs plus *Rathkea octopunctata*. Once ingestion occurred at least equivalent to the mean number of ingested prey of each type observed in nature (Table 1), each medusan was isolated in filtered seawater and examined every 10 min until defecation was completed and the gut empty. All experiments were carried out at 4°C, near ambient temperature in Bedford Basin in early May.

Daily rations were calculated from such digestion times and from the average number of prey found in the manubrium of each type of medusan and converted to daily carbon ingested per medusan, knowing the carbon content of each prey type, using the following equation modified from Larson (1987a):

$$(1)\quad R = C_{med} \times 24/D_t$$

where R = daily ration in (micrograms carbon per medusan per day), C_{med} = carbon content in (micrograms) in the gut of the medusan, and D_t = digestion time (hours).

The potential impact of predation by medusans was estimated from prey density and the daily ration for each medusan species. We express this impact in micrograms carbon ingested per cubic metre per day and also as percentage of total carbon weight of mesozooplankton.

Results

Species Composition and Numerical Abundance

Species richness among geltinousa predators was very low in contrast with their relatively high numerical abundance (Fig. 1). Only five species of hydromedusans were present, *Sarsia princeps*, *Euphysa tentaculata*, *Rathkea octopunctata*, *Cosmetira* sp., and *Aglantha digitale*, and one scyphomedusan, *Aurelia aurita*. The ctenophore *Pleurobrachia* sp. and the chaetognath *Sagitta elegans* were also observed in the upper 30 m.

Hydromedusans always represented more than 50% of the total medusan dry weight and carbon. Numerically, the most important was *Rathkea octopunctata*, the population of which increased from 2 individuals·m^{-3} at the end of March to a maximum of 95·m^{-3} in May (Fig. 1A). *Aglantha digitale* adults, at 11·m^{-3}, were the most abundant hydromedusans in mid-March, but they disappeared by the end of April (Fig. 1A). For the remainder of our survey, we found only juvenile *Aglantha* in the tows. Other hydromedusans were less abundant and showed little variation in numbers except for *Cosmetira* sp. which did not appear until early May and was never very numerous.

The scyphomedusan *Aurelia aurita* was initially represented by only a few (0.2–0.9·m^{-3}) small individuals (1–3 cm in diameter). The average diameter increased progressively to 10 to 15 cm, but the population density never greatly exceeded 1 individual·m^{-3} (Fig. 1A). In May and June, *Aurelia aurita* could be seen at the surface, but their average concentration remained low.

Among other gelatinous predators, ctenophores could occur in concentrations <0.1 individual·m^{-3} in early spring and increased to >1·m^{-3} in early June (Fig. 1B). *Sagitta elegans* were most abundant in the upper 30 m in March when we found up to 30·m^{-3} of individuals <1 cm long.

Elemental Composition

The mean dry weights of mature specimens of the three smaller hydromedusans were about the same, but their carbon

TABLE 1. Mean number of prey of each type, with carbon content, used to compute digestion times and specific daily ration.

	Prey							
	Copepods		Eggs		*Rathkea*		Total	
Predator	No.	Carbon (μg·prey^{-1})	No.	Carbon (μg·prey^{-1})	No.	Carbon (μg·prey^{-1})	No.	Carbon (μg)
Sarsia princeps	1.5	5.47	—	—	—	—	1.5	8.20
Euphysa tentaculata	2	5.47	—	—	—	—	2	10.94
Rathkea octopunctata								
Adults	1.5	5.47	—	—	—	—	1.5	8.20
Juveniles	1	5.47	—	—	—	—	1	5.47
Cosmetira sp.	3	5.47	—	—	—	—	3	16.41
Aglantha digitale	1	5.47	2	0.56	—	—	3	6.59
Aurelia aurita	5	5.47	5	0.56	10	10	20	130.15

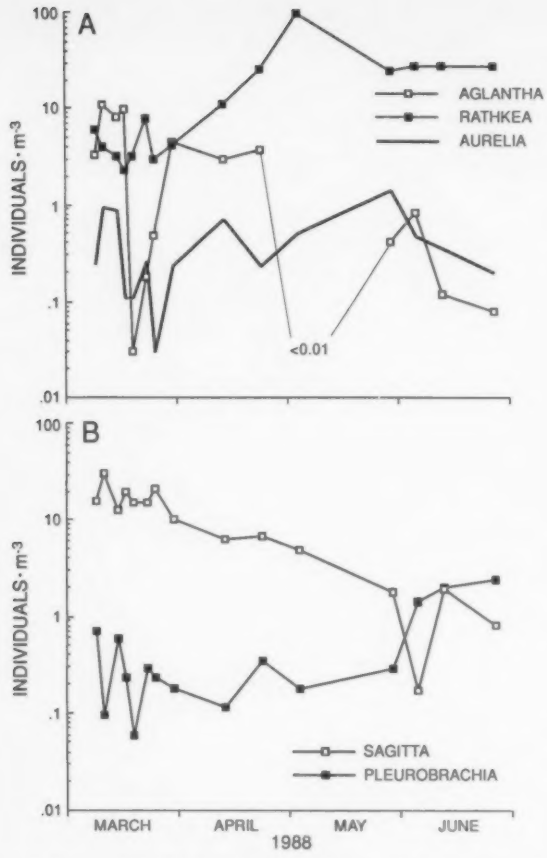


FIG. 1. Seasonal distribution of gelatinous predators in the upper 30 m of Bedford Basin between March 8 and June 29, 1988. (A) Numerical abundance of the principal medusan species; (B) numerical abundance of the ctenophore *Pleurobrachia* sp. and the chaetognath *Sagitta elegans*.

and nitrogen weights differed considerably (Table 2). The carbon concentration in *Rathkea octopunctata* was more than twice that of *Sarsia* and *Euphysa*, and the nitrogen content 7–10 times greater. As a consequence, the C:N ratios were strikingly different among the three species. Juvenile *Rathkea octopunctata* had even higher proportions of carbon and nitrogen to dry weight than the larger individuals but the C:N ratio remained the same.

Because there was considerable change in the height of the bell in *Aglantha digitale* over the course of our observations, we used linear regression to express the change in size to dry weight and carbon and nitrogen contents. The range in bell height was roughly from 4.5 to 13 mm and we have calculated the appropriate values for the maximum and minimum size observed (Table 2). In terms of dry weight the smallest *Aglantha* are about the same size as the other small hydromedusans and have somewhat higher carbon and nitrogen contents than *Sarsia* and *Euphysa*, but substantially lower than that of *Rathkea*. The proportions do not change greatly as the individuals get larger.

We have made the same type of calculation for the extremes in umbrella diameter in *Aurelia aurita* observed during our survey, but in this species, larger animals appear to have a disproportionately large amount of nitrogen relative to the other species examined including *Rathkea*.

Medusan Diets

Of approximately 2500 medusans examined, about 600 had empty guts. Thus, 1900 individuals contained from one to several prey, 4465 in total. Hydromedusans contained up to three prey items, but *Aurelia aurita* sometimes contained more than 20. Of the organisms counted, 65% were copepods, generally between 250 and 500 μm long, belonging to the genera *Acartia* and *Pseudocalanus*. Eggs of ctenophores, chaetognaths, and fish, along with some of copepods and other crustaceans, were the second most important component in the diet. Other prey (fish larvae, veligers, copepod nauplii, etc.) contributed less than 10% to the gut contents.

Diets varied somewhat among species (Table 3). Copepods dominated in guts of the smaller hydromedusans and only copepods were found in two species. *Aglantha digitale* and *Aurelia aurita* consumed a wider range of zooplankton types and less than 50% copepods. Zooplankton eggs, generally >200 μm in diameter, were much the preferred food for *Aglantha* and the second most important food in *Rathkea*. Only a few *Aurelia aurita* contained more than 20 prey, which we somewhat arbitrarily defined as a "full gastric pouch." Among accumulated prey in their gastric pouches were copepods, fish larvae, veligers, and some microplankton (diatoms, other algae, ciliates), which were not observed in other species. *Aurelia* also ingested significant numbers (34% of its diet) of its potential competitor, *Rathkea octopunctata*.

Medusan diets also changed over the course of the spring. Over the first eight sampling dates (March 8 to April 5) when numbers of invertebrates eggs were relatively low in the water column (Fig. 2A), the fraction >200 μm in the jellyfish diet was disproportionately large (Fig. 2B), suggesting positive selection, which was supported by the "log of odds ratio" (Gabriel 1978). Later, eggs became less important in the medusan diet, eventually contributing only 1 or 2% (Fig. 2B), while the copepod population decreased in abundance and carbon biomass (Fig. 2A, 3A) apparently under increasing medusan predation.

Digestion Times and Digestion Rates

The range and variation in the digestion data were relatively low considering that different species of predators with rather different feeding patterns and prey preferences were used. *Aglantha digitale* had the shortest digestion time, just under 2 h, and there was no difference between copepods and eggs (Table 4). Adults seemed to digest copepods slightly faster than juveniles in *Rathkea octopunctata*, but the difference was probably not significant. We assumed that *Rathkea octopunctata* digested eggs at the same rate that it digested copepods, as was the case in *Aglantha digitale*. The other hydromedusans digested copepods at about the same rate ($1/D_t$), about 0.5, except for *Cosmetira* in which the rate was about 0.3 (Table 4). Size of the predator had no effect on digestion in the scyphozoan *Aurelia*, which had the lowest rate, 0.26, but because of the larger amount of food in its gut, doubtless digested and assimilated more carbon and nitrogen per unit time than the hydromedusans that shared the environment with it.

Daily Ration

The mean carbon weight of the copepod prey in our experiments was 5.47 μg (SD = 1.67) and for eggs was 0.56 (0.12)

TABLE 2. Elemental composition of medusans. C, carbon in μg; N, nitrogen in μg; DW, dry weight in μg; *D*, diameter in cm; *H*, height of the bell in mm; *n*, number of observations; standard deviation in parentheses. The elemental compositions (C and N) of *Aglantha digitale*[a] and *Aurelia aurita*[b] are calculated by linear regressions as functions of the medusan size.

Taxon	*n*	DW	C	N	C:N	C (%DW)	N (%DW)
Hydromedusae							
Sarsia princeps	9	29.84 (1.05)	1.99 (0.10)	0.67 (0.04)	2.97	6.67 (0.21)	2.25 (0.24)
Euphysa tentaculata	10	28.48 (1.57)	1.69 (0.35)	0.38 (0.17)	4.45	5.86 (0.82)	1.36 (0.65)
Rathkea octopunctata							
Adults	7	23.96 (1.73)	6.05 (1.36)	3.89 (0.89)	1.56	25.08 (3.98)	16.24 (3.02)
Juveniles	12	10.03 (0.976)	3.92 (0.27)	2.49 (0.33)	1.57	38.37 (5.32)	24.73 (1.29)
Cosmetira sp.	10	58.97 (1.44)	7.79 (1.42)	2.48 (0.30)	3.14	13.21 (0.88)	4.35 (1.04)
Aglantha digitale							
13 mm	—	60.67	5.72	2.99	1.91	9.43	4.93
4.5 mm	—	24.06	2.42	1.07	2.26	10.06	4.45
Scyphomedusae							
Aurelia aurita							
15 cm	—	8488	201.48	155.38	1.30	2.37	1.83
2 cm	—	2365	77.72	20.52	3.79	3.29	0.87

[a]DW (μg) = 4.307 H + 4.675 (n = 10; r = 0.803; P<0.05); C = 0.389 H + 0.668 (n = 10; r = 0.887; P<0.05); N = 0.226 H + 0.054 (n = 10; r = 0.900; P<0.05).

[b]DW (mg) = 0.471 D + 1.423 (n = 8; r = 0.975; P<0.05); C = 9.516 D + 58.696 (n = 8; r = 0.842; P<0.05); N = 10.374D − 0.223 (n = 8; r = 0.983; P = 0.05).

TABLE 3. Diet of medusans in percentage of total observed during spring 1988 (March–June). Cop, copepods; N, copepod nauplii; V, veligers; FL, fish larvae; R.o., *Rathkea octopunctata*; Micro, microplankton (diatoms, ciliates,) etc.).

Taxon	*n* (empty)	Cop	N	Eggs	V	FL	R.o.	Micro
Hydromedusae								
Sarsia princeps	54 (18)	100	—	—	—	—	—	—
Euphysa tentaculata	106 (18)	75	10	10	—	—	—	—
Rathkea octopunctata	1436 (355)	52.23	3.48	40.38	3.82	—	—	—
Cosmetira sp.	13 (−)	100	—	—	—	—	—	—
Aglantha digitale	499 (120)	19.30	2.10	75.52	3.10	—	—	—
Scyphomedusae								
Aurelia aurita	189 (85)	44	4	12.02	<0.50	<0.35	34.11	5.96

(Table 1). For hydromedusans the number of prey ingested per day varied from 9 to 26 (Table 5). The projected daily rations for hydromedusans exceeded 1500% of their own carbon weight except for *Rathkea octopunctata*, which has a similar ingestion rate but a higher proportion of carbon as a function of dry weight. Juvenile *Rathkea* also consumed proportionately more than the adults of the same species. When feeding on eggs, the ration of *Aglantha digitale* was about that of larger *Aurelia*, but its combined ration, with copepods included, was also over 1500%. We calculated the ration for an *Aurelia aurita* with an 8-cm umbrella diameter on the basis of the time to digest a full gastric pouch of 20 prey of mixed type (Table 1) which yielded a value about 400% of body carbon burden; however, smaller individuals consumed proportionally more (Table 5).

Carbon Content of Prey and Predators and Potential Predatory Impact

Mesozooplankton carbon weight in the upper 30 cm of Bedford Basin increased rapidly from 5.9 mg C·m^{-3} in early March to a peak of 13 mg C·m^{-3} at the end of April (Fig. 3A). The medusan stock followed a similar pattern of development but reached its maximum in early May (Fig. 3B). In March and early April, when the medusan standing stock was around 0.06 mg C·m^{-3}, their calculated impact on the potential prey was 10% or less, regardless of prey concentration, but by early May, when they reached maximum concentration (0.493 mg C·m^{-3}), their ration was 59% of the prey stock (Fig. 3B). The zooplankton carbon concentration then decreased abruptly and remained stable around 6 mg C·m^{-3} until the end of June (Fig. 3A).

Discussion

Possible Errors

The projected daily rations for most of the species of predators examined here are considerably higher than those commonly found in the literature, especially for hydromedusans (Larson 1987a; Båmstedt 1990). It is therefore expedient to look at possible sources of error that might make our observations unrealistic. Larson (1987a, 1987b) studied a similar community of predators in a somewhat larger and deeper, but otherwise similar, fjord (Saanich Inlet) on Vancouver Island (British Columbia, Canada). He used two different nets of approximately the same mesh as ours (200 and 750 μm), but 0.5 m in diameter, also towed vertically over the upper 25 m. Our study was modelled on his in many respects, and therefore, we examined the same set of factors that he did as sources of potential bias, i.e. (1) net feeding, (2) loss of gut

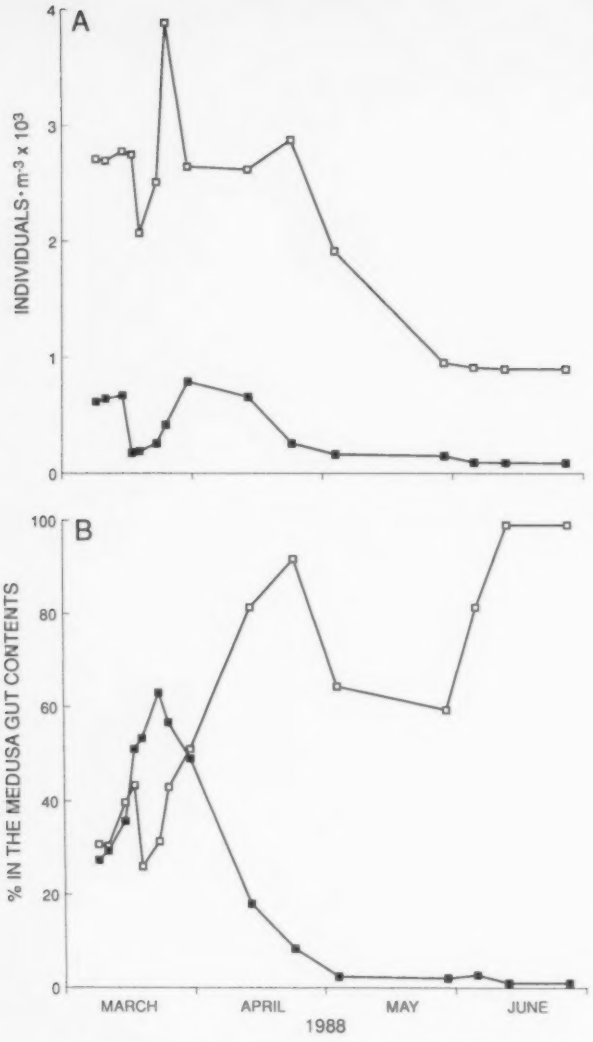


FIG. 2. Seasonal abundance of zooplankton and eggs and their contribution to medusan gut contents in upper 30 m of Bedford Basin in spring 1988. (A) Seasonal abundance of copepods (□) and eggs of other zooplankton (■); (B) copepods (□) and eggs (■) as percentages of medusan gut contents.

contents after collection, (3) inaccurate estimates of predator and prey den sities, (4) variability in digestion time, and (5) diel variations in ingestion rates (Larson 1987a). To this list we add an additional consideration, (6) differences in the vertical distribution of predators and potential prey.

Net feeding

Larson (1987b) compared the gut contents of the same set of predators in 200- and 750-μm nets, assuming that a larger fraction of predators from the finer net would contain a potentially larger number of prey if net feeding had taken place, but there was no statistical difference between the sample sets. We did not make this same comparison, but used only the coarse net samples for determination of gut contents. Because the tows were always <5 min in duration from launching the net to pres-

TABLE 4. Laboratory analysis of digestion time (h) for medusans. Cop, copepods 200–500 μm long; FP, full gastric pouch. Standard deviation in parentheses.

Taxon	*n*	Prey	Digestion time (Dt) (h)	Digestion rate ($1/D_t$)
Hydromedusae				
Sarsia princeps	12	Cop	2.12 (0.22)	0.47
Euphysa tentaculata	11	Cop	1.94 (0.18)	0.52
Rathkea octopunctata				
Adults	14	Cop	2.22 (0.29)	0.45
Juveniles	9	Cop	2.55 (0.32)	0.39
Cosmetira sp.	10	Cop	3.25 (0.17)	0.31
Aglantha digitale	12	Cop	1.73 (0.26)	0.57
	9	Eggs	1.82 (0.27)	0.55
Scyphomedusae				
Aurelia aurita	8	FP	3.85 (0.24)	0.26

TABLE 5. Projected daily ration of medusans during spring. Cop, copepods; FP, full gastric pouch; % C·d^{-1}, % of the body carbon weight of the predator ingested daily.

Taxon	Prey·d^{-1}		μg C·d^{-1}	% C·d^{-1}
Hydromedusae				
Sarsia princeps	Cop	16.98	92.88	>2000
Euphysa tentaculata	Cop	24.74	135.34	>2000
Rathkea octopunctata				
Adults	Cop	16.21	88.66	243.96
Juveniles	Cop	9.41	51.46	376.53
Cosmetira sp.	Cop	22.15	121.15	1500
Aglantha digitale	Eggs	26.37	14.76	500–750
	Cop	13.85	75.74	>2000
Scyphomedusae				
Aurelia aurita	FP	3.83	498.70	400–750

ervation and all predators took more time than this to completely engulf prey during observations of feeding behaviour and during gut-filling prior to digestion measurements, we do not consider net feeding to have been a factor in our results.

Loss of gut contents

We did not specifically address the problem of lost gut contents, but this would not have increased our estimates of daily ration unless it occurred during measurements of digestion time, in which case it would almost certainly have been noticed by the observer.

Sampling and prey and predator concentrations

Sampling was carried out only over the upper 30 m of Bedford Basin, which is the approximate depth of the seasonal mixed layer (Krauel 1969), because the majority of the neritic, semipermanent residents, both prey and predators, occur there (Conover and Mayzaud 1975; Atherton 1979). The principal exception is mature *Sagitta elegans* which are generally found near the bottom during the day. Gelatinous organisms in this study were always present in low abundance relative to the copepod and other crustaceans. During the spring bloom in mid-March, copepods reached numerical densities up to 4000·m^{-3} whereas the medusan density never exceeded 100·m^{-3}. We did not enumerate the smaller zooplankton in detail but they generally belong to five genera: *Pseudocalanus*, *Acartia*, *Temora*, *Eurytemora*, and *Oithona*. The number of prey, 1000–4000·m^{-3}, in 1988 was of the same order as Poulet (1978)

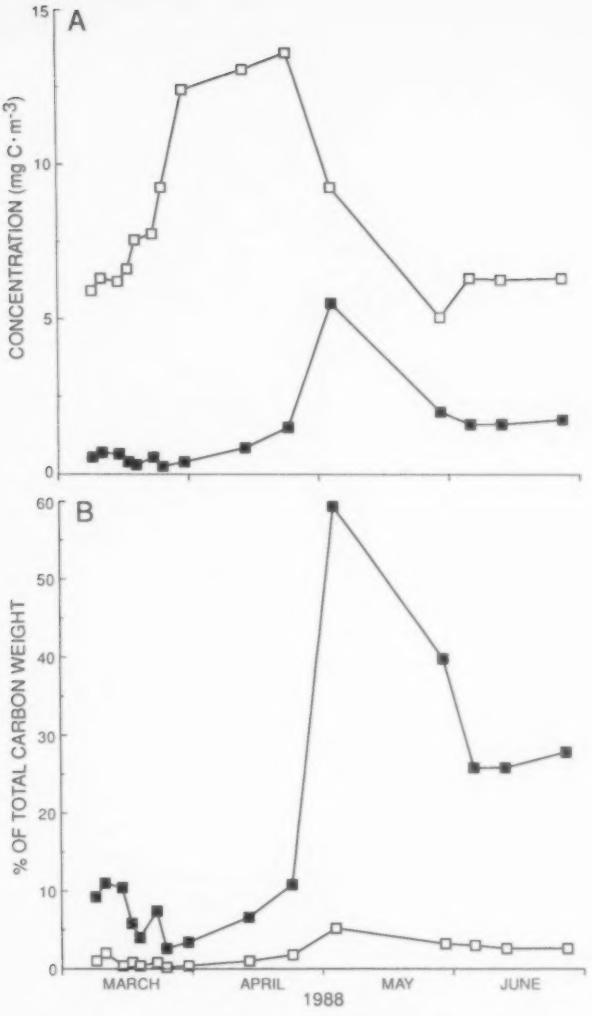


FIG. 3. Concentration of mesozooplankton and of medusans and potential predatory impact by medusans in the upper 30 m of Bedford Basin in spring 1988. (A) Total carbon biomass of the mesozooplankton (□) and amount of carbon ingested by medusans (■); (B) carbon weight of medusans as a percentage of total mesoplankton carbon weight (□) and their consumption as percentage of total mesoplankton carbon weight (■).

found in 1970 and 1971 with a similar net at the same season and station and somewhat higher than the numbers (100–1000·m^{-3}) observed by Conover and Mayzaud (1975) in 1975.

Digestion time

The use of gut contents as a means of calculating an in situ feeding rate depends on determining a digestion or gut turnover time or rate of gut passage, but none of these determinations are easily accomplished. Models have been proposed to examine the digestive process (e.g. Penry and Jumars 1987), but we still lack information necessary for a useful solution in the case of gelatinous predators. Determining digestion time following prefeeding of the predator is only one of several approximations which have been tried to get at a usable rate. Comparison of our data with similar estimates from the literature (Table 6) really does little but emphasize the variability. Digestion time will vary with biological factors such as the size of the meal, probably with its quality, as well as with several physical factors, and possibly the response to some or all the factors can be modified by previous experience of the predator. Our method relied on determining the mean meal size and then feeding predators a meal of at least those dimensions prior to initiating the timing of digestion. Our observations were all made at 4°C which was probably somewhat warmer than the mean temperature for March but lower than that for June in Bedford Basin. Over the spring months the vertical distribution of temperature changes rapidly as stability becomes established, and therefore, choosing a specific temperature at which to make the digestion measurements is not straightforward. Our measurements, like all those before, are a compromise with reality, but they have given consistent results which are certainly more applicable to our environment than any others in Table 6.

Diel feeding patterns and vertical distributions of predator and prey

We did not address either of these concerns specifically. Atherton (1979) examined diel vertical migration of the total zooplankton community in Bedford Basin on seven dates over the course of 1 yr, and three of his sets of observations fell within the window of our observations but in a different year. Among the prey organisms in our tows, only *Pseudocalanus* occasionally occurred deeper than 30 m during diel migrations and then only during March among the months that we both sampled. In an earlier study of diel migration in *Pseudocalanus* in Bedford Basin, only the youngest stages showed a clear pattern of depth change in May (Lock 1968). We have no data on vertical movements of any of the medusans but *Sagitta elegans* is a strong migrator (Pearre 1973; Atherton 1979). Sameoto (1973) believed that *Sagitta elegans* was the most important predator in Bedford Basin, but his use of a high-speed sampler (modified Icelandic) may have damaged the smaller medusans beyond recognition (Sameoto 1971). It is possible that prey and predator were differently distributed within the upper 30 m at certain times of the day and our sampling methods would have smeared any such signal. We did standardize our sampling to late morning, a time of day when encounters between prey and predator might be expected to be minimal if any diel feeding or migration pattern of the usual sort prevailed. Therefore, we feel that diel changes and distributional differences would probably have no effect or would increase contacts between prey and predator and therefore would increase the impact of the gelatinous predators on other zooplankton rather than diminish it.

Seasonal Distribution of Gelatinous Predators

Rathkea octopunctata was the dominant hydromedusan from mid-March to the end of June and accounted for 80% of the carbon biomass of jellyfish in May. Russell (1953) described it as a winter–spring form, which appears first in January and becomes very abundant by April. The species reproduces asexually, by budding from the manubrial wall, as well as sexually (Chun 1896), and it can produce large populations quickly as a consequence. A peak population of 250 animals·m^{-3} was observed in July and August in the Barents Sea (Zelickman et al. 1969). In Bedford Basin, all *Rathkea octopunctata* collected in March and April had at least two primary asexual buds (mean 3.5). Some individuals had both mature gonads and manubrial buds. The buds were first released as juveniles at the

TABLE 6. Digestion time of some medusans from Bedford Basin, with additional information on the same genera from other locations. Cop, copepods; Egg, invertebrate eggs >200 μm; EL, euphausiid larvae; FL, fish larvae; FP, full gastric pouch (20 mixed prey).

Taxon	Prey	Digestion time (h)	Temperature (°C)	Reference
Hydromedusae				
Cosmetira sp.	Cop	3–4	4	Present work
Aglantha digitale	Egg	<2	4	Present work
	Cop	<2	4	
Rathkea octopunctata	Cop	4–9	<12	Plotnikova 1961
	Cop	2–3	4	Present work
	EL	3–5	<12	Plotnikova 1961
	FL	14–20	<12	Plotnikova 1961
Sarsia tubulosa	Cop	3–4	<12	Plotnikova 1961
	EL	1–2	<12	Plotnikova 1961
Sarsia princeps	Cop	2–3	4	Present work
	FL	1.5	12	Fraser 1969
Euphysa tentaculata	Cop	2	4	Present work
Scyphomedusae				
Aurelia aurita	FP	3–4	4	Present work
	FL	2	12	Fraser 1969
	FL	3.5–9.5	10–12	Möller 1980b
	FL	4–6	10–13	Bailey and Batty 1983
	FL(10[a])	18.9 (2.3)[b]	5	Heeger and Möller 1987
		12.2 (2.6)	10	
		8.2 (1.4)	15	
		3.8 (0.9)	22	

[a]10 prey used.
[b]Standard deviation for 10 predators.

end of March and reached a maximum in early May ($65 \cdot m^{-3}$). By June, all mature *Rathkea* had disappeared from the basin. Also noteworthy, *Rathkea octopunctata* accounted for about 60–70% of the total zooplankton population in Bedford Basin at the beginning of June 1975, a year in which the total zooplankton population was also relatively low (Conover and Mayzaud 1975).

The seasonal behaviour of the other medusans in Bedford Basin was generally in agreement with their distribution elsewhere. Despite being the most common medusan in the basin in mid-March, *Aglantha digitale* were never abundant. Mature individuals (11 mm bell height) were present until the end of April when they largely disappeared (Fig. 1A) to be replaced by smaller individuals (5–6 mm bell height) in late May. Migration to greater depths after maturation and spawning has been described by Smedstad (1972) and Williams and Conway (1981) for this species, which might account for the disappearance of the mature individuals observed in Fig. 1A and appearance of what was probably the new generation by May. If so, spawning took place earlier and at colder temperatures in Bedford Basin (March, 2–3°C) than at station India (May, 9°C) in the North Atlantic (Williams and Hopkins 1975). In any event, only juveniles were found during the remainder of the spring period in Bedford Basin. As for *Aurelia aurita*, which can be found from the subarctic to the tropics (Möller 1980a), the animals were quite small in March but their average diameter increased by May. The pattern of development of this medusan is characterized by a dormant phase in winter, followed by rapid growth in spring and early summer (Möller 1979). Our observations are also similar to those of Möller (1980a) in Kiel Bight and Fancett and Jenkins (1988) in Port Phillip Bay (Victoria, Australia) in summer.

Chemical Composition

Because our calculations of daily ration and predatory impact are based on carbon weight, a comparison of our chemical composition data with that in the literature is in order. Earlier estimates of carbon and nitrogen weights of hydromedusans range from 3 to 15% and from 1 to 5% of dry weight, respectively (Curl 1962; Beers 1966; Omori 1969; Ikeda 1974; Larson 1986). Our results were in the same range, being 5.9–13.2% of dry weight for carbon and 1.3–4.9% for nitrogen (Table 2) in every case except for *Rathkea octopunctata*. For this species, carbon was 25% and nitrogen 16% of dry weight which seems remarkably high. The medusan umbrella generally has a lower organic content than the gonads and tentacles (Shenker 1985; Larson 1986). Probably the presence of primary buds contributed significantly to the carbon and nitrogen contents of the individual *Rathkea octopunctata* from Bedford Basin. The juveniles, which resemble the buds from which they were derived, had the highest carbon and nitrogen concentrations of all.

In Bedford Basin, the organic content of *Aurelia aurita* was of the same order as that observed by others for scyphomedusans, i.e. 3–5% carbon and 1–4% nitrogen (Curl 1962; Beers 1966; Shenker 1985; Larson 1986).

The mean C:N ratio for 11 hydromedusan species from the Northeast Pacific calculated from the data in Larson (1986) was 3.56 and for *Sarsia princeps* and *Aglantha digitale* was 3.56 and 3.7, respectively. Our C:N values tended to be somewhat lower, and those for *Rathkea octopunctata* and *Sarsia princeps* considerably so. However, where our values differ from those in the literature, the discrepancy is generally in the nitrogen concentration. Our carbon estimates usually agree well and therefore are not a source of bias in comparing our observations with estimates of predation impact in the literature.

Diet and Selective Predation

Selective predation was apparently exhibited by medusans during the spring period in Bedford Basin (Table 3). In April and early May, invertebrate eggs were strongly preferred to copepods by the medusan community (Fig. 2). Swimming behaviour of medusans relative to that of the prey seems to determine their fishing capability and prey selection (Mills 1981). Gerritsen and Strickler (1977) and Greene et al. (1986) have argued that diets of predators depend on prey concentration, their vulnerability, and on the predator–prey encounter probability, which in part depends on the relative swimming speeds, relative size of both predator and prey, and the hunting strategy of the predator. Thus, "ambush predators" should be more efficient in catching fast-moving prey whereas "cruising" ones should catch slow-moving prey more efficiently.

Copepods numerically dominated the mesozooplankton in Bedford Basin over the spring period and they are mostly strong swimmers, suggesting greater vulnerability to ambush predators. Our own observations on local hydromedusans in a 20-L tank suggested that *Rathkea octopunctata*, *Aglantha digitale*, and *Euphysa tentaculata* were mainly ambush-type predators, along with *Cosmetira* sp., which used a slightly different strategy, first swimming up and then drifting down with tentacles extended. *Sarsia princeps* swam actively during its feeding with continuous pulsations of the umbrella, but in Bedford Basin, it consumed exclusively copepods. In Saanich Inlet, *Sarsia princeps* fed almost entirely on copepods and euphausiid larvae (Larson 1987a, 1987b).

Pelagic eggs, primarily from other gelatinous zooplankton, were a major part of the diet of *Rathkea octopunctata* and *Aglantha digitale* (Table 3). Both predators mostly drift with extended tentacles, and therefore should encounter active copepods more often, but they seemed to ingest relatively immobile eggs. According to Larson (1987b), turbulence probably moves nonmotile prey relative to predators, thus increasing encounter rates. In Saanich Inlet (Larson 1987a) and in Oslofjord (Smedstad 1972), *Aglantha digitale* also consumed mostly eggs. An alternative explanation might be that the jellyfish and eggs in early spring are more closely associated physically within their habitat than are jellyfish and copepods. Whatever the explanation for this paradox, in Bedford Basin, hydromedusan predation pressure was eventually transferred to the copepods as eggs became relatively more scarce.

Aurelia aurita seems to capture whatever prey it encounters while swimming (Southward 1955; Stoecker et al. 1987). They may significantly reduce fish larval (Möller 1984; de Lafontaine and Leggett 1988) and copepod populations (Fraser 1969; Möller 1979, 1980b; Lindahl and Hernroth 1983). In Bedford Basin their diet was mixed, but we found $<10\%$ microplankton in their gastric pouches, although Smetacek (1981) and Stoecker et al. (1987) believed that they can be important grazers on microplankton.

Daily Rations

Daily ration (micrograms carbon per animal per day) generally varies with the size, weight-specific ration decreasing with increasing weight of predator. In our experiments, the daily rations exceeded 750% of predator carbon weight except for relatively large *Aurelia aurita* and for *Rathkea octopunctata*, which has a disproportionately large fraction of both carbon and nitrogen in its tissue compared with the other gelatinous predators (Table 2). In laboratory feeding experiments in which high concentrations of prey were presented, a number of gelatinous predators, including medusans, have been shown to consume more than 10 times their body weight in a day (Walter 1976; Reeve 1980; Kremer 1979; Stanlaw et al. 1981; Matsakis and Nival 1989), but these rates may not always reflect natural situations. Many invertebrate carnivores have the capacity to gorge when food is available while surviving extended periods of starvation by self-digestion and shrinkage because they have limited alternative storage capacity (Conover 1978). Coelenterates in particular have prodigious appetites, and the hydroid *Clava multicornis* will literally eat itself to death if given the opportunity (Paffenhöfer 1968). Gelatinous predators in the pelagic zone probably have a large stomach capacity to take advantage of episodic periods of high prey density (Cosper and Reeve 1975; Reeve 1980) such as might well be found in a fjord in spring.

Predatory Impact

Gelatinous zooplankton (medusans, ctenophores, siphonophores) usually consume less than 10% of their prey resource in a day, but they can exceed 50% and decimate food supplies (Alldredge 1984; Larson 1987b). In Bedford Basin, the average impact for the 4-mo period was 15.8% which fell between these values, but over the spring season, it ranged from 2% in March to at least 59% in early May, and they apparently could remove more than 25% of the zooplankton carbon daily through June (Fig. 3B).

An increase in medusan carbon weight during spring coincided with the decrease in total carbon biomass (Fig. 3A), suggesting that these predators were part of the mechanism regulating the zooplankton standing stock. Of these, *Rathkea octopunctata* was the dominant form, with high population numbers and rapid reproductive rates. It always consumed at least 50% of the carbon consumed by medusan species. With the decrease in the copepod population later in May, medusan populations also declined (Fig. 3B). Although food limitation is one possibility, zooplankton concentrations did not fall below early March concentrations. The decrease in *Rathkea* abundance in mid-May corresponded with an increase in numbers of *Aurelia aurita* (Fig. 1A), and also in their mean size. During this period, *Rathkea* was a major component of the gastric pouches of *Aurelia*, and we believe that predation by *Aurelia aurita* may ultimately contribute to the disappearance of *Rathkea* observed in this and other years (R. J. Conover and S. A. Poulet, unpubl. data). There are at least three earlier reports of *Rathkea octopunctata* being consumed by *Aurelia aurita* (Husing 1956; Loginova and Perzova 1967, both cited in Arai and Jacobs 1980; Lebour 1923).

The net decline in zooplankton carbon (Fig. 3) was doubtless the combined effect of all predators in the water column. Neither the chaetognath *Sagitta elegans*, except for a few juveniles, nor the ctenophore *Pleurobrachia*, during winter and spring, was abundant in our tows (Fig. 1B), but by the end of June, *Pleurobrachia* had increased to 2.5 individuals·m^{-3} and might have represented serious competition for medusans, especially for *Sarsia princeps*, *Euphysa tentaculata*, and *Cosmetira*, which disappeared about this time. Earlier in the spring, predation by *Rathkea octopunctata* and *Aglantha digitale* on ctenophore eggs probably limited their population development. To assess the predatory impact of chaetognaths on Bedford Basin zooplankton, we calculated a daily carbon ration for *Sagitta elegans*, using our population data, assuming that its feeding

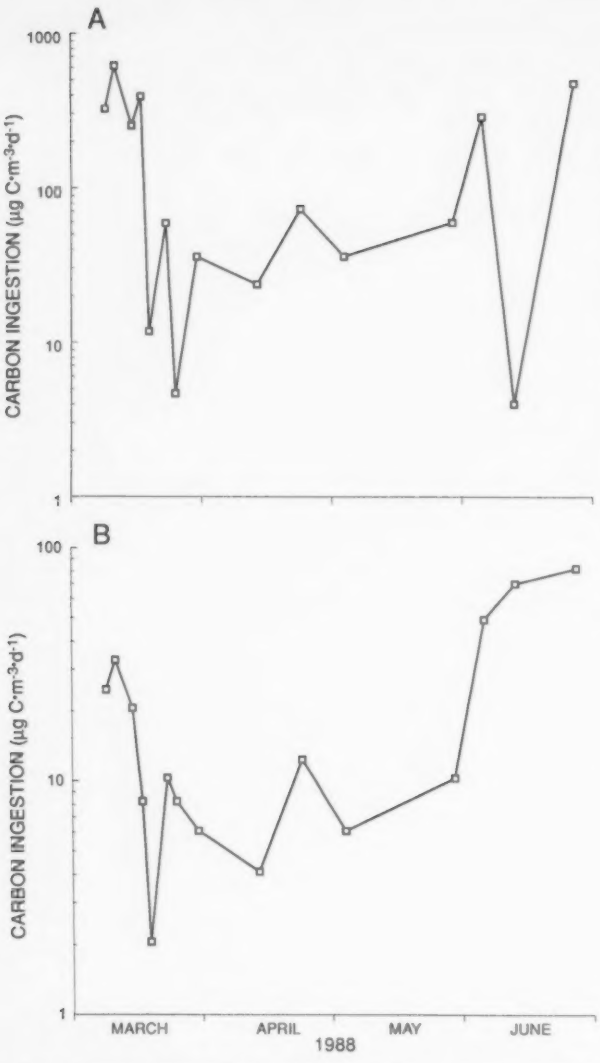


FIG. 4. Potential impact (per individual) of other gelatinous predators in the upper 30 m of Bedford Basin on mesozooplankton during spring 1988. (A) *Sagitta elegans*; (B) *Pleurobrachia* sp.

behaviour was similar to that for *Sagitta enflata* (Feigenbaum 1979). To compare the impact of the ctenophore, we assumed that daily ration was 35 µg $C \cdot d^{-1}$, the average ration for *Pleurobrachia bachei* in culture at 12–15°C (Hirota 1972). Our peak estimated impact for *Sagitta elegans*, 600 µg $C \cdot m^{-3} \cdot d^{-1}$, was about the same as that calculated for the total medusan population at the beginning of March, but rather than increase, it decreased rapidly (Fig. 4A). Considering that *Sagitta enflata* is a subtropical species and might have a considerably shorter digestive time, and therefore a potentially larger impact than *Sagitta elegans*, the predatory role of chaetognaths would not seem to be very significant during the period of our study. Similarly, our estimate of predation impact for *Pleurobrachia* over the same period, also in all probability an overestimate, would suggest an even smaller effect on zooplankton populations than for *Sagitta* (Fig. 4B).

The nonsaturating functional response (de LaFontaine and Leggett 1988) and reproductive potential of the medusans seem to impact on both prey and other predator populations in Bedford Basin. In the early spring, when temperatures are still quite cold, medusans, some of which can reproduce rapidly by budding, would seem to have a reproductive advantage over the copepods, which must pass through 12 developmental stages before contributing to the next generation. At this time, medusans also consume considerable numbers of eggs of potential competitors such as chaetognaths and ctenophores. Later, as medusan populations become well established, the proportion of eggs eaten decreases (perhaps because the threat of competition from other noncoelenterate predators is lessened), while the number of copepods consumed increases (Fig. 2B). By altering selection pressure on certain prey, by whatever mechanism, hydromedusans can potentially control zooplankton dynamics, as we have shown for spring in Bedford Basin, but whether they can maintain a dominant role in regulating zooplankton population dynamics throughout the productive season is problematic at this time.

Acknowledgments

We thank Don Knox and John Conrad who designed and constructed the jellyfish net to our very rough specifications. Roger Belanger supplied some of the equipment and contributed importantly to the development of the silouette photographic system. We are also grateful to Jeff Anning, Mark Hodgson, and Brian Irwin who participated in the field work at different times. Dr. Gabriel Gorsky kindly reviewed the manuscript during its preparation.

References

ALLDREDGE, A. L. 1984. The quantitative significance of gelatinous zooplankton as pelagic consumers, p. 407–433. *In* M. R. J. Fasham [ed.] Flow of energy and materials in marine ecosystems. Theory and practice. Plenum Press, New York, NY.

ARAI, M. N., AND J. R. JACOBS. 1980. Interspecific predation of common Strait of Georgia planktonic coelenterates: laboratory evidence. Can. J. Fish. Aquat. Sci. 37: 120–123.

ATHERTON, W. C. 1979. An annual study of the vertical migration patterns of zooplankton in Bedford Basin, Nova Scotia. M.Sc. thesis, Dalhousie University, Halifax, N.S. 107 p.

BAILEY, K. M., AND R. S. BATTY. 1983. A laboratory study of predation by *Aurelia aurita* on larval herring (*Clupea harengus*): experimental observations compared with model prediction. Mar. Biol. 72: 295–301.

1984. Laboratory study of predation by *Aurelia aurita* on larval cod, flounder, plaice and herring: development and vulnerability to capture. Mar. Biol. 83: 287–291.

BÅMSTEDT, U. 1990. Trophodynamics of the scyphomedusae *Aurelia aurita*. Predation rate in relation to abundance, size and type of prey. J. Plankton Res. 12: 215–229.

BEERS, J. R. 1966. Studies on the chemical composition of the major zooplankton groups in the Sargasso Sea off Bermuda. Limnol. Oceanogr. 11: 520–528.

BRACONNOT, J. C. 1985. Confection et utilisation de photogrammes pour les études de croissance, de développement et d'abondance de populations d'espèces pélagiques gélatineuses. C.R. Acad. Sci. Paris Ser. III 300 (15): 563–565.

CHUN, C. 1896. Die Knospungsgesestze der proliferirenden Medusen. Chap. I, p. 3–52, plates 1 and 2. Atlantis biologische Studien über pelagische Organismen. Bibliotheca Zoologica. Band VII, Heft 19.

CONOVER, R. J. 1978. Transformation of organic matter, p. 221–499. *In* O. Kinne [ed.] Marine ecology. Vol. IV. Dynamics. John Wiley, Chichester, U.K.

CONOVER, R. J., AND P. MAYZAUD. 1975. Respiration and nitrogen excretion of neritic zooplankton in relation to potential food supply, p. 151–163. 10th European Symposium on Marine Biology, Ostend, Belgium, Sept. 17–23, 1975. 2.

1984. Utilization of phytoplankton by zooplankton during the spring bloom in a Nova Scotia inlet. Can. J. Fish. Aquat. Sci. 41: 232–244.

COSPER, T. C., AND M. R. REEVE. 1975. Digestive efficiency of the chaetognath *Sagitta hispida*. J. Exp. Mar. Biol. Ecol. 17: 33–38.

CURL, H. 1962. Analysis of carbon in marine plankton organisms. J. Mar. Res. 20: 181–188.

DAAN, R. 1986. Food intake and growth of *Sarsia tubulosa* (Sars, 1835) with quantitative estimates of predation on copepod populations. Neth. J. Sea Res. 20: 67–74.

1989. Factors controlling the summer development of copepod populations in the southern bight of the North Sea. Neth. J. Sea Res. 23: 305–322.

DE LAFONTAINE, Y., AND W. C. LEGGETT. 1987. Effect of container size on estimates of mortality and predation rates in experiments with macrozooplankton and larval fish. Can. J. Fish. Aquat. Sci. 44: 1534–1543.

1988. Predation by jellyfish on larval fish: an experimental evaluation employing in situ enclosures. Can. J. Fish. Aquat. Sci. 45: 1173–1190.

FANCETT, M. S., AND G. P. JENKINS. 1988. Predatory impact of Scyphomedusae on ichthyoplankton and other zooplankton in Port Phillip Bay. J. Exp. Mar. Biol. Ecol. 116: 63–77.

FEIGENBAUM, D. L. 1979. Daily ration and specific daily ration of the chaetognath *Sagitta enflata*. Mar. Biol. 54: 75–82.

FRASER, J. H. 1969. Experimental feeding of some medusae and Chaetognatha. J. Fish. Res. Board Can. 26: 1743–1763.

FULTON, R. S., AND R. G. WEAR. 1985. Predatory feeding of the hydromedusae *Obelia geniculata* and *Phialela quadrata*. Mar. Biol. 87: 479–54.

GABRIEL, W. L. 1978. Statistics of selectivity, p. 62–66. *In* S. J. Lipovsky and C. A. Simensted [ed.] Gutshop '78. Washington Sea Grant Publ., Seattle, WA.

GERRITSEN, J., AND J. R. STRICKLER. 1977. Encounter probabilities and community structure in zooplankton: a mathematical model. J. Fish. Res. Board Can. 34: 73–82.

GORSKY, G., S. DALLOT, J. SARDOU, R. FENNAUX, C. CARRÉ, AND I. PALAZOLLI. 1988. C and N composition of some northwestern Mediterranean zooplankton and micronekton species. J. Exp. Mar. Biol. Ecol. 124: 133–144.

GREENE, C. H., M. R. LANDRY, AND B. C. MONGER. 1986. Foraging behavior and prey selection by the ambush entangling predator *Pleurobrachia bachei*. Ecology 67: 1493–1501.

GRICE, G. D., R. P. HARRIS, M. R. REEVE, J. F. HEINBOKEL, AND C. O. DAVIS. 1980. Large scale enclosed water-column ecosystem, an overview of food web I, the final CEPEX experiment. J. Mar. Biol. Assoc. U.K. 60: 401–414.

HARGRAVE, B. T., G. C. HARDING, K. F. DRINKWATER, T. C. LAMBERT, AND W. G. HARRISON. 1985. Dynamics of the pelagic food web in St. Georges Bay, southern Gulf of St. Lawrence. Mar. Ecol. Prog. Ser. 20: 221–240.

HARRIS, R. P., M. R. REEVE, G. D. GRICE, G. T. EVANS, V. R. GIBSON, J. R. BEERS, AND B. K. SULLIVAN. 1982. Trophic interactions and production processes in natural zooplankton communities in enclosed watercolumns, p. 353–387. *In* G. D. Grice and M. R. Reeve [ed.] Marine mesocosms: biological and chemical research in experimental ecosystems. Springer Verlag, New York, NY.

HEEGER, T., AND H. MOLLER. 1987. Ultrastructural observations on prey capture and digestion in the scyphomedusa *Aurelia aurita*. Mar. Biol. 96: 391–400.

HIROTA, J. 1972. Laboratory culture and metabolism of the planktonic ctenophore, *Pleurobrachia bachei* A. Agassiz, p. 465–484. *In* A. Y. Takenouti [chief ed.] Biological oceanography of the northern North Pacific Ocean. Idemitsu Shoten, Tokyo, Japan.

HUNTLEY, M. E., AND L. A. HOBSON. 1978. Medusa predation and plankton dynamics in a temperate fjord, British Columbia. J. Fish. Res. Board Can. 35: 257–261.

HUSING, J. O. 1956. Zur Frage der Ernahrung der Ohrenqualle *Aurelia aurita* L. (Scyphozoa, Semaeostomae). Wiss. Z. Martin Luther Univ. Halle-Wittenberg Math. Naturwiss. Reihe 5(3): 479–482.

IKEDA, T. 1974. Nutritional ecology of marine zooplankton. Mem. Fac. Fish. Hokkaido Univ. 22: 1–97.

KRAUEL, D. P. 1969. Bedford Basin data report — 1967. Fish Res. Board Can. Tech. Rep. 120: 84 p.

KREMER, P. 1979. Predation by the ctenophore *Mnemiopsis leidyi* in Narrangansett Bay, Rhode Island. Estuaries 2: 97–105.

LARSON, R. J. 1986. Water content, organic content and carbon and nitrogen composition of medusae from the northeast Pacific. J. Exp. Mar. Biol. Ecol. 99: 107–120.

1987a. Daily ration and predation by medusae and ctenophores in Saanich Inlet, B.C. Canada. Neth. J. Sea Res. 21: 35–44.

1987b. Trophic ecology of planktonic gelatinous predators in Saanich Inlet, British Columbia: diets and prey selection. J. Plankton Res. 9: 811–820.

LEBOUR, M. V. 1923. The food of planktonic organisms II. J. Mar. Biol. Assoc. U.K. 13: 70–92.

LINDAHL, O., AND L. HERNROTH. 1983. Phyto-zooplankton community in coastal waters of western Sweden — an ecosystem off balance? Mar. Ecol. Prog. Ser. 10: 119–126.

LOCK, A. R. 1968. A laboratory and field study of the possible role of temperature in vertical migrations of the copepod *Pseudocalanus minutus* (Krøyer). M.Sc. thesis, Dalhousie University, Halifax, N.S. 81 p.

LONGIOVA, N. P., AND N. M. PERZOVA. 1967. Some data on ecology of feeding of pelagic Coelenterata in the White Sea. Issled. Fauny Morei 7(15): 21–28. (In Russian)

MATSAKIS, S., AND P. NIVAL. 1989. Elemental composition and food intake of *Phialidium* hydromedusae in the laboratory. J. Exp. Mar. Biol. Ecol. 130: 277–290.

MILLS, C. E. 1981. Diversity of swimming behaviors in hydromedusae as related to feeding and utilization of space. Mar. Biol. 64: 185–189.

MÖLLER, H. 1979. Significance of coelenterates in relation to other plankton organisms. Meeresforschung 27: 1–18.

1980a. Population dynamics of *Aurelia aurita* medusae in Kiel Bight, Germany (FRG). Mar. Biol. 60: 123–128.

1980b. Scyphomedusae as predators and food competitors of larval fish. Meeresforschung 28: 90–100.

1984. Reduction of a larval herring population by jellyfish predators. Science (Wash., DC) 224: 621–622.

OMORI, M. 1969. Weight and chemical composition of some important oceanic zooplankton in the North Pacific Ocean. Mar. Biol. 3: 4–10.

PAFFENHÖFER, G.-A. 1968. Nahrungsaufnahme, Stoffumsatz und Energiehaushalt des marinen Hydroidenpolypen *Clava multicornis*. Helgol. wiss. Meeresunters. 18: 1–44.

PEARRE, S. JR. 1973. Vertical migration and feeding in *Sagitta elegans* Verril. Ecology 54: 300–314.

PENRY, D. L., AND P. A. JUMARS. 1987. Modeling animal guts as chemical reactors. Am. Nat. 129: 69–96.

PLATT, T., AND R. J. CONOVER. 1971. Variability and its effect on the 24h chlorophyll budget of a small marine basin. Mar. Biol. 10: 52–65.

PLOTNIKOVA, E. D. 1961. On the diet of medusae in the littoral of eastern Murman, p. 153–156. *In* M. M. Kamshilov [ed.] Hydrological and biological features of the shore waters of Murman. Akad. Nauk USSR Kolsk. Fil. (In Russian)

POULET, S. A. 1978. Comparison between five coexisting species of marine copepods feeding on naturally occurring particulate matter. Limnol. Oceanogr. 23: 1126–1143.

PURCELL, J. E. 1985. Predation on fish eggs and larvae by pelagic cnidarians and ctenophores. Bull. Mar. Sci. 37: 739–755.

REEVE, M. R. 1980. Comparative experimental studies on the feeding of chaetognaths and ctenophores. J. Plankton Res. 2: 381–393.

ROFF, J. C., K. MIDDLEBROOK, AND F. EVANS. 1988. Long-term variability in North Sea zooplankton off the Northumberland coast: productivity of small copepods and analysis of trophic interactions. J. Mar. Biol. Assoc. U.K. 68: 143–164.

RUSSELL, F. S. 1953. The medusae of the British Isles. Cambridge University Press, Cambridge, U.K. 529 p.

SAMEOTO, D. D. 1971. Macrozooplankton biomass measurements in Bedford Basin, 1969–1971. Fish. Res. Board Can. Tech. Rep. 282: 238 p.

1973. Annual life cycle and production of the chaetognath *Sagitta elegans* in Bedford Basin, Nova Scotia. J. Fish. Res. Board Can. 30: 333–344.

SHENKER, J. M. 1985. Carbon content of the neritic scyphomedusa *Chrysaora fuscescens*. J. Plankton Res. 7: 169–173.

SMEDSTAD, O. M. 1972. On the biology of *Aglantha digitale rosae* (Forbes), Coelenterata, Trachymedusae in the Oslo fjord. Norw. J. Zool. 20: 111–135.

SMETACEK, V. 1981. The annual cycle of protozooplankton in the Kiel Bight. Mar. Biol. 63: 1–11.

SOUTHWARD, A. D. 1955. Observations on the ciliary currents of the jelly-fish *Aurelia aurita* L. J. Mar. Biol. Assoc. U.K. 34: 201–216.

STANLAW, K. A., M. R. REEVE, AND M. A. WALTER. 1981. Growth, food and vulnerability to damage of the ctenophore *Mnemiopsis mccradyi* in its early life history stages. Limnol. Oceanogr. 26: 224–234.

STOECKER, D. K., A. E. MICHAELS, AND L. H. DAVIS. 1987. Grazing by the jellyfish, *Aurelia aurita*, on microzooplankton. J. Plankton Res. 9: 901–915.

WALTER, M. A. 1976. Quantitative observations on the nutritional ecology of the ctenophores with special reference to *Mnemiopsis mccradyi*. M.Sc. thesis, University of Miami, Miami, FL. 70 p.

WILLIAMS, A., AND D. V. P. CONWAY. 1981. Vertical distribution and seasonal abundance of *Aglantha digitale* (Muller) (Coelenterata: Trachymedusae)

and other planktonic invertebrates in the northeast Atlantic Ocean. J. Plankton Res. 3: 634–643.

WILLIAMS, A., AND C. C. HOPKINS. 1975. Biological sampling at ocean weather station India (59°00′N, 19°00′W) in 1973. Ann. Biol. Cons. Perm. Int. Explor. Mer 30: 60–62.

ZELICKMAN, E. A., V. I. GELFAND, AND M. A. SHIFRIN. 1969. Growth, reproduction and nutrition of some Barents Sea hydromedusae in natural aggregations. Mar. Biol. 4: 167–173.

An Approach to Modeling Crustacean Egg-Bearing Fractions as a Function of Size and Season

Victor R. Restrepo

University of Miami, Rosenstiel School of Marine and Atmospheric Science, Cooperative Institute for Marine and Atmospheric Studies, 4600 Rickenbacker Causeway, Miami, FL 33149, USA

and Reg A. Watson

Northern Fisheries Centre, P.O. Box 5396, Cairns Mail Centre 4871, Queensland, Australia

Restrepo, V. R., and R. A. Watson. 1991. An approach to modeling crustacean egg-bearing fractions as a function of size and season. Can. J. Fish. Aquat. Sci. 48: 1431–1436.

We present an approach to the analysis of crustacean egg production ogives with emphasis on detecting seasonal trends. The relationship between the proportion of gravid females (by size) and season is a prerequisite to the estimation of egg production potentials of populations. The basic method consists of relating, for each sample, the proportion of berried females with their size through a three-parameter logistic function where the asymptote may be less than 1. We then provide guidance for detecting seasonal trends in the estimates of the parameters for the individual samples. This is accomplished by restricting the basic model such that some parameters are considered to be either fixed for all samples or as simple functions of time or environmental variables such as temperature. Parameter estimates are obtained via maximum likelihood methods, and comparisons between alternative models are presented graphically and using likelihood ratio tests. We illustrate the approach and its application with data for a tropical shrimp, *Penaeus esculentus*, from northern Australia.

Nous présentons une approche pour l'analyse des enveloppes d'oeufs de crustacés qui insiste sur la détection des tendances saisonnières. Le rapport entre la proportion de femelles gravides (par taille) et la saison est un prérequis pour l'évaluation du potentiel de production d'oeufs des populations. La méthode de base est basée sur l'établissement de rapports, pour chaque échantillon, entre la proportion des femelles porteuses d'oeufs avec leur taille grâce à une fonction logistique à trois paramètres dont l'asymptote peut être inférieure à un. Nous donnons ensuite des conseils permettant de déceler les tendances saisonnières dans les évaluations des paramètres d'échantillons individuels. On y arrive en restreignant le modèle de base de façon à ce que certains paramètres soient considérés comme étant soit fixes pour tous les échantillons, ou soit de simples fonctions du temps de variables environnementales comme la température. Des évaluations de paramètres sont obtenues par la méthode de la vraisemblance maximum et des comparaisons entre plusieurs modèles possibles sont présentées graphiquement et utilisent des tests de rapports de ressemblance. Nous illustrons cette approche et son application avec des données obtenues pour une crevette tropicale, *Penaeus esculentus*, provenant du nord de l'Australie.

Received April 25, 1990
Accepted February 20, 1991
(JA554)

Reçu le 25 avril 1990
Accepté le 20 février 1991

Determination of an individual's average egg production is essential to obtain estimates of the reproductive potential of a population. Physiologically, a crustacean's production of eggs at any given time is the result of numerous complex interactions between internal and external factors. Among the internal factors are size (age), biochemical and metabolic changes, and hormonal factors. Environmental factors may include temperature, light, salinity, and food (Sastry 1983).

In modeling egg production at the population level for stock assessment purposes, it is often useful to calculate the reproductive potential of every size class in the population separately (see Campbell and Robinson 1983; Fogarty and Idoine 1988; Cobb and Caddy 1989). For tropical and subtropical species that spawn more than once annually, it is particularly important to consider seasonal changes in spawning frequency. For instance, the average number of eggs produced by females of size x at time t, E_{xt}, can be modeled as

$$(1) \quad E_{xt} = N_{xt}B_{xt}G_{xt}$$

where N_{xt} = number of females of size x present at time t, B_{xt} = fraction of females of size x that are carrying eggs at time t (berried females), and G_{xt} = number of eggs produced by a female of length x in each egg batch (fecundity).

Typically, N_{xt} can be obtained from research surveys or fishery-dependent data (e.g. via virtual population analysis), or it may simply be a variable in a simulation model. Given samples of individual egg counts and size measurements, knowledge about the form of and estimation of the relevant parameters in G_{xt} can be straightforward. For many decapods, fecundity is a linear or exponential function of body length.

In contrast, knowledge about the form of the function relating berried fractions with size and season may not be obvious. Ideally, the data used to postulate an appropriate empirical relationship should provide information on two aspects: (a) the proportion of physiologically mature animals (defined here as those capable of producing viable gametes) and (b) the proportion of these that are actually producing eggs at a given time.

Reproductive maturity is generally a nonlinear function of size (Sastry 1983; Hartnoll 1985; Wenner et al. 1985). In species that extrude eggs only once during the course of a brief

reproductive season, a maturity–size relationship can be attained if an egg production ogive occurs during the reproductive season. A plot of proportion of berried females in each size class typically results in an *S*-shaped relationship with an asymptote approaching 1.0 for the largest sizes (see Wenner et al. 1974). Problems may be encountered, however, with some species in which not all physiologically mature females actually extrude eggs. In species that lay eggs several times during a longer reproductive season, the relationship between maturity and size cannot be estimated in the same fashion because not all mature females will be ovigerous at all times. Plots of the egg production ogives will also be sigmoid, but the observed asymptotes will differ from 1.0, depending on the time at which the samples are taken.

In this study we propose a simple approach to model berried fractions as a function of size and season. The general model assumes that egg production ogives obtained during sequential samples are independent of each other. We also present a maximum likelihood method to estimate the parameters of such a model and illustrate its application with data for a tropical shrimp, *Penaeus esculentus* (Haswell, 1879), in Torres Strait, Australia.

Model

Consider a sample taken during the course of a brief time period (e.g. 1 mo or less) in which a large number of females are measured and the presence or absence of eggs in each individual is recorded. The fraction berried in each size, B_{xt}, is estimated by

$$\frac{r_{xt}}{N_{xt}}$$

where r is the number of females with eggs and N is the total-number of females. Considering the binomial nature of the data (i.e. eggs are either present or absent in an individual), the probability distribution for the fraction berried in each length group is (Welch and Foucher 1988; Schnute and Richards 1990):

$$(2)\quad \Pr(B_{xt}) = \binom{N_{xt}}{r_{xt}} (B_{xt})^{r_{xt}} (1 - B_{xt})^{N_{xt} - r_{xt}}.$$

The likelihood associated with the sample is the product of the probability distributions at each length class. Given that individuals are measured in lengths indexed 1 to M, the likelihood is

$$(3)\quad \Lambda = \prod_{x=1}^{M} \Pr(B_{xt}).$$

We propose the use of a simple, three-parameter sigmoid function to model changes in the proportion berried as a function of x (and also as a function of t in the next section):

$$(4)\quad B_{xt} = \frac{C_t}{1 + e^{(a_t - b_t x)}}.$$

Disregarding the numerator in equation (4), this is a simple logistic equation that is commonly employed to study maturity as a function of size in finfish and crustaceans. The parameter $C_t (0 \leq C_t \leq 1)$ allows for the maximum fraction of berried females to be less than 1. Note that other equations such as a modified logistic (Welch and Foucher 1988), a cumulative normal (Wenner et al. 1974), or a function of the hyperbolic tangent (Polovina 1989) can be used instead. Ratkowsky (1983) presented a comparison between the estimation properties of the parameters in equation (4) and other parameterizations of the logistic curve.

For a given sample, the parameters a_t, b_t, and C_t can be estimated by finding the values that maximize the logarithm of the likelihood function (from equations (3) and (4)):

$$(5)\quad \ln(\Lambda) = \sum_{x=1}^{M} \ln\binom{N_{xt}}{r_{xt}} + r_{xt} \ln\left(\frac{C_t}{1 + e^{(a_t - b_t x)}}\right) + (N_{xt} - r_{xt}) \ln\left(1 - \frac{C_t}{1 + e^{(a_t - b_t x)}}\right).$$

The binomial coefficient, the first term in the right-hand side of equation (5), can be ignored because its value is independent of the parameters a_t, b_t, and C_t. Estimates of the parameter values that maximize the log-likelihood function can be obtained with a numerical search algorithm. In the examples below, we used the implementation of the simplex search of Nelder and Mead (1965) given in Press et al. (1987). There are a number of ways to derive variance estimates and confidence regions for the parameter estimates (Kendall and Stuart 1973; Seber and Wild 1989). In this study, we used the inverse of the large sample information matrix, evaluated at the maximum likelihood estimates, to approximate the variance–covariance matrix of the parameter estimates.

Extensions of the model to cases in which egg production ogives are obtained for S time periods are straightforward. The obvious first choice involves the use of equation (5) to estimate three parameters independently for each sample. From a modeling point of view, it may not be desirable to require $3 \cdot S$ parameters to model the fractions of berried females during S time periods. It is, however, useful to follow this approach as a first step because plots of the parameter estimates over time may reveal a well-defined seasonal behavior.

Following such an exploratory analysis, further restrictions can be imposed on the simple model to reduce the number of parameters. For instance, one possibility is that the location and curvature of the logistic function (given by parameters a and b) remain relatively unchanged while the asymptote varies with time. Equation (4) becomes

$$(6)\quad B_{xt} = \frac{C_t}{1 + e^{(a - bx)}}$$

and the likelihood function is given by

$$(7)\quad \Lambda = \prod_{t=1}^{S} \prod_{x=1}^{M} \Pr(B_{xt}).$$

In this case, a total of $S + 2$ parameters are estimated: one C_t for every sample plus one a and one b. Note that while in the previous model the parameters can be estimated independently for each sample, the parameters in equation (7) must be estimated simultaneously. More general formulations, requiring the estimation of more parameters, could also be hypothesized by specifying time-specific a's or b's.

The adequacy of a restricted model can be assessed by plotting the predicted functions against the observed berried percentages for each sample. Likelihood ratio tests (Seber and Wild 1989) can also be used for this purpose. If the analyses suggest

TABLE 1. Sample sizes (N) for the *Penaeus esculentus* data used, and results of likelihood ratio tests between fits of two-parameter (asymptote = 1.0) and three-parameter (asymptote estimated) logistic functions; $\log(\Lambda)_3$ and $\log(\Lambda)_2$ are the values of the log-likelihood function for the two fits, respectively. Values of the test statistic ($\chi^2 = 2[\log(\Lambda)_2 - \log(\Lambda)_3]$) greater than 3.84 indicate that the varying-asymptote model is preferable at the 5% level.

Month	N	$\log(\Lambda)_3$	$\log(\Lambda)_2$	χ^2
Jan. 1986	291	−154.36	−155.38	2.03
Feb. 1986	547	−246.58	−257.75	22.34
Mar. 1986	400	−232.52	−236.62	8.20
Apr. 1986	535	−235.27	−236.93	3.31
May 1986	342	−177.21	−181.09	7.76
June 1986	407	−139.73	−147.33	15.20
July 1986	104	−55.32	−57.05	3.46
Aug. 1986	282	−137.26	−137.48	0.44
Sept. 1986	85	−35.28	−36.15	1.75
Oct. 1986	173	−89.43	−92.17	5.49
Nov. 1986	236	−123.92	−134.41	20.99
Dec. 1986	303	−140.26	−145.02	9.51
Jan. 1987	352	−172.20	−179.36	14.33
Feb. 1987	558	−206.64	−226.19	39.11
Mar. 1987	478	−122.29	−122.29	0.00
Apr. 1987	269	−40.00	−40.00	0.00
May 1987	2507	−1070.03	−1077.49	14.90
June 1987	990	−398.90	−401.21	4.63
July 1987	239	−121.82	−123.47	3.30
Aug. 1987	167	−87.15	−87.34	0.38
Oct. 1987	418	−236.36	−252.08	31.43
Nov. 1987	310	−163.41	−178.23	29.64
Dec. 1987	450	−219.00	−247.20	56.40
Jan. 1988	674	−301.56	−321.37	39.61
Feb. 1988	790	−400.64	−414.72	28.16
Apr. 1988	650	−268.06	−270.81	5.49
June 1988	353	−50.07	−51.33	2.53
Sept. 1988	221	−78.09	−81.43	6.66
Oct. 1988	373	−203.46	−209.56	12.19
Nov. 1988	272	−148.66	−148.73	0.15
Jan. 1989	491	−153.84	−166.70	25.72
Feb. 1989	736	−144.43	−156.57	24.27
Mar. 1989	404	−150.87	−154.16	6.59
Apr. 1989	843	−380.20	−380.31	0.21
May 1989	452	−217.55	−217.78	0.45
June 1989	369	−145.08	−147.76	5.35

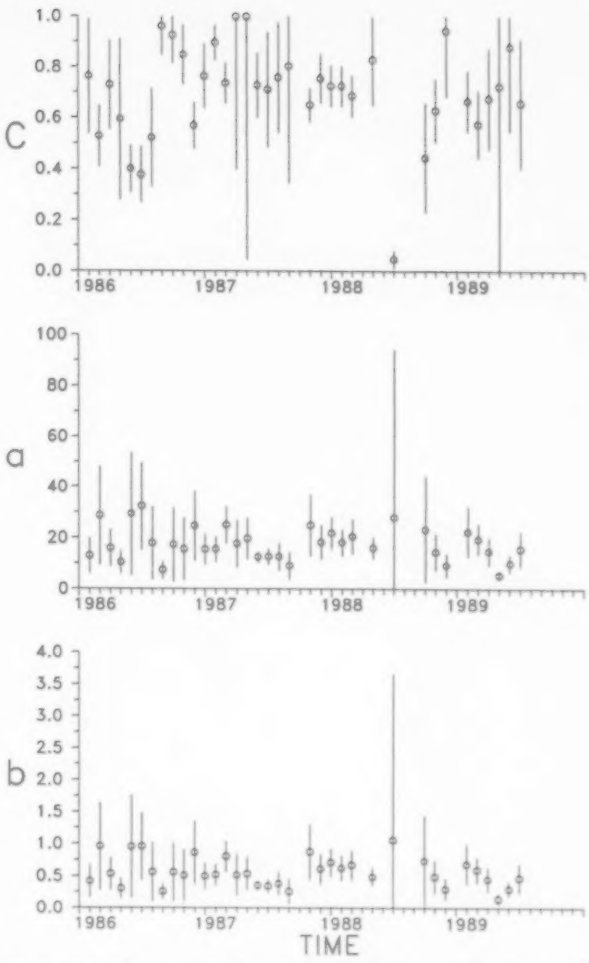


FIG. 1. Monthly trends in the estimates of the parameters C_t, a_t, and b_t (equation (4)) fitted to the 36 samples of *Penaeus esculentus* data. The vertical bars represent approximate 95% confidence limits.

that the model given by equation (6) is adequate, it is possible to further simplify the model to fewer than $S + 2$ parameters. For instance, if temperature data or other relevant environmental indices are available, a plot of C_t against these other data may reveal the presence of a linear or nonlinear relationship. Thus, if a second-degree polynomial seems appropriate, the C_t in equation (6) could be substituted by $(c_0 + c_1 T + c_2 T^2)$ where T denotes the variable of interest (such as temperature). In this case, only five parameters would require estimation (c_0, c_1, c_2, a, and b), regardless of the number of samples.

Seasonal trends in C_t could be dealt with in a number of different ways. For instance, it may be reasonable to assume that C_t will vary between months but remain constant from year to year for any particular month. This would entail estimating 12 C_t's or one for each month of the year. Because the limited number of years of data restrict our ability to obtain consistent estimates of monthly C_t's, this particular approach has not been adopted. In this study, the annual peaks and troughs in egg production potential appear to be sinusoidal in nature. A useful model for the asymptote is thus

$$(8)\quad C_t = d_0 + d_1 \cos\left(2\pi \frac{t}{12}\right) + d_2 \sin\left(2\pi \frac{t}{12}\right)$$

where t takes on the sequential values for the months when sampling took place starting at $t = 1$. Similarly, numerous other models could be postulated where the parameters in the equation relating egg-bearing fractions to size are either fixed, sample specific, or functions of environmental variables. Examples are given below to illustrate the application of some of those already mentioned.

Data and Biological Background

Egg production data for *Penaeus esculentus* were available for 36 monthly samples taken near Warrior Reef in Torres Strait, northern Australia, between January 1986 and June 1989. Each female was measured to the nearest millimetre (car-

apace length) and those with ovary stages III and IV (Tuma 1967) were considered ripe. Monthly sample sizes averaged 474 females (Table 1), with carapace lengths ranging between 15 and 52 mm.

In *Penaeus esculentus*, a single spawning usually occurs after fertilization and before the next molt. At the population level, molting and spawning appear to take place asynchronously throughout the year and at a nearly constant level throughout each lunar month (Crocos 1985). Crocos (1985) suggested that in order to obtain a reliable index of spawning frequency, the duration of the ripe stage should be shorter than the period of sampling. Our monthly data meet this criterion because the duration of ripe stages is reported to be approximately 66% of the mean intermolt period of 28 d. If our samples had represented shorter time periods (e.g. days), then biased estimates of spawning activity would be more likely.

Results

Estimates of the parameters in equation (4) for each of the 36 monthly data sets followed the trends in the data closely (Fig. 1 and 2). Estimates of the asymptote, C_t, ranged from a low of 0.046 to a high of 1.0 (Fig. 1). Estimates of parameters a_t and b_t were also variable (Fig. 1) and highly correlated (r_{ab} = 0.981 for the 36 samples).

We tested the possibility that a conventional two-parameter model would adequately describe the data by fixing C_t to a value of 1.0 for every sample, instead of estimating it, and comparing the resulting fits with those of equation (4) (Fig. 1) via likelihood ratio tests. The null hypothesis that $C_t = 1.0$ was rejected in 23 (64%) of the samples (Table 1). Of the remaining 13 samples, eight had estimates of C_t whose 95% confidence limits included 1.0 (see Fig. 1). Thus, it is expected that the null hypothesis would fail to be rejected in these eight samples. Fisher's test for combining independent significance levels (Fisher 1970, p. 99–101) indicated that the probability of the aggregate of the 36 tests in Table 1 occurring by chance is less than 0.0001 ($\chi^2_{72} = 542.79$). Overall, it is apparent then that the three-parameter model fits the data better than does the two-parameter logistic function with a fixed asymptote equal to 1.

We then examined the possibility of reducing the number of parameters necessary to model egg production potential for the 36 samples. We did this by estimating an individual asymptote for each sample and common a and b values for all samples

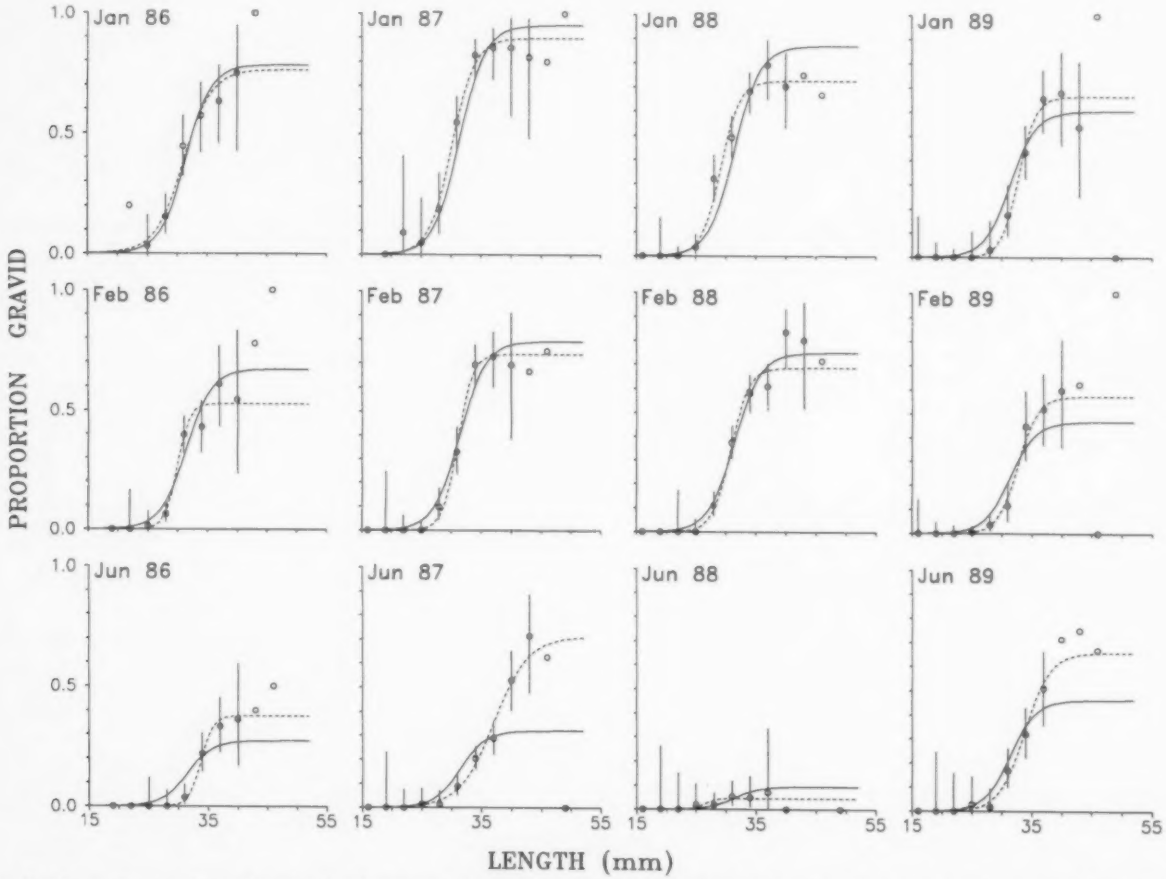


FIG. 2. Observed proportions of egg-bearing females (circles) and fitted equations (lines) for 12 samples of *Penaeus esculentus*. For clarity, the raw data were grouped into 3-mm intervals (ungrouped data were used for parameter estimation). Fractions made up of 10 or more observations include approximate 95% binomial confidence limits (vertical lines) computed with the Paulson–Takeuchi method described by Fujino (1980). The broken lines represent the individual fits of equation (4) to the samples. The solid lines represent the fit of the more constrained model (equation (6)) in which the asymptote varies but the curvature parameters remain fixed and are estimated with data from all available samples.

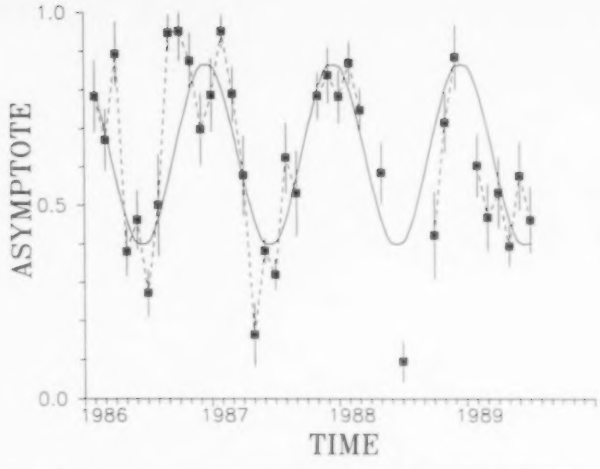


FIG. 3. Estimates of the asymptote for two models of egg-bearing fractions fitted to 36 samples of *Penaeus esculentus*. The broken line and solid squares show the estimates of the asymptote from the model given by equation (6), in which one value is obtained for every sample (vertical bars are approximate 95% confidence limits). The solid line represents the fit of a more constrained model (equation (8)) in which the asymptote is a sinusoidal function of time.

(i.e. 38 parameters were estimated with equation (6)). Trends in the estimates of the asymptote are shown in Fig. 3. The estimates of a and b were 14.56 and 0.463, with variances of 0.196 and 0.0002, respectively. A likelihood ratio test indicated that the fit of equation (4) to the individual monthly samples (108 parameters, $\log(\Lambda) = -7247.45$) may be statistically preferable to that of the more constrained model given by equation (6) (38 parameters, $\log(\Lambda) = -7499.44$) (likelihood ratio statistic $\chi^2_{72} = 503.98$, $P < 0.0001$).

Upon visual examination, the fit of the constrained model appeared to be reasonable for most samples (a subset of the fits is shown in Fig. 2). However, for the samples taken during August 1986 and January 1988, the constrained model tended to underestimate berried percentages for the smaller sizes and to overestimate them for the larger sizes. The opposite occurred with the samples taken in June 1986, March 1987, May 1987, and June 1987. In particular, the results for these last two samples were poor considering that they contained the largest number of observations (2507 and 990, respectively).

While the observed monthly variability is more accurately described by individual fits of equation (4) to each sample, equation (6) may be adequate to represent the general seasonal trends in the observed data. The latter has intuitive appeal because the only sample-specific parameter in it is the asymptote. Thus, variations in the estimated values of this asymptote can be thought of as seasonal changes in the egg production potential of the population. (Note that changes in actual egg production must also take into consideration size structure and population numbers.)

We also estimated the parameters of the sinusoidal model for the asymptote given by equation (8). The estimates of a and b were 14.64 and 0.465, respectively, values that are similar to those obtained with the 38-parameter model (equation (6)). In general, the asymptote values predicted by the sinusoidal function coincided well with the estimates from equation (6), although the simple function failed to predict the low egg production potentials typical of winter months such as June 1988 (Fig. 2 and 3).

Discussion

The conventional method of using annual samples and assuming the egg-bearing fractions are asymptotic to unity may be sufficient for species with brief reproductive seasons. The approach we have presented requires more data and is computationally intensive but is more useful for species that reproduce throughout the year and exhibit within-year fluctuations in reproductive potential. Use of a model with a seasonal component can provide insight into important management questions. For instance, incorporation of a relationship for monthly egg-bearing fractions into an egg-per-recruit model can aid in determining the optimum time to set seasonal closures for a fishery when the goal is to enhance the reproductive output of a stock.

The basic model (equation (4)) is most useful when one desires to explain accurately the observed variability in the proportion of berried females by size, for a given sample. When modeling equilibrium egg production potential, this model is undesirable because it requires too many parameters. In contrast, the more restricted models (e.g. equation (6) and (8)) sacrifice precision but provide estimates that are more useful in an equilibrium modeling framework. To illustrate this idea, consider the examples above where equations (4) and (8) were fitted to the 36 monthly samples of egg-bearing females. Given additional data for fecundity relationships and the size frequency distributions every month, the monthly magnitudes of egg production can be estimated with equation (1). These values could then be used in conjunction with recruitment estimates to examine the presence of a stock–recruitment relationship. The berried proportions used in such a study should preferably be the sample-specific estimates (equation (4)). In contrast, estimates of the sinusoidal function (equation (8)) would be preferable for a simulation of equilibrium egg production per recruit because they consist of fewer parameters and predict a long-term relationship. Currently, this approach may have limited applicability because the large number of samples necessary to capture seasonal fluctuations are not typically available for most crustacean fisheries. However, quantifying reproductive data is a relatively simple task with some species and such measurements can be incorporated into a routine sampling program.

As we have illustrated with some examples, other models that fall between the two extremes in the previous paragraph are straightforward to formulate. The parameters could be treated as constants or as functions of time or of some environmental variable. In any case, the applicability of the selected model would be largely dictated by its intended purpose.

Acknowledgments

We are grateful to David Die, Clay Porch, John Hoenig, and Michael Prager for their useful comments and encouragement. We also thank Drs. Alan Campbell and David Welch and an anonymous referee for their comments and suggestions. Support for this study was provided by the Queensland Department of Primary Industries, the Queensland Fish Management Authority, and through the Cooperative Institute for Marine and Atmospheric Studies by National Oceanic and Atmospheric Administration Cooperative Agreement No. NA85-WCH-06134.

References

CAMPBELL, A., AND D. G. ROBINSON. 1983. Reproductive potential of three American lobster (*Homarus americanus*) stocks in the Canadian Maritimes. Can. J. Fish. Aquat. Sci. 40: 1958–1967.

COBB, J. S., AND J. F. CADDY. 1989. The population biology of decapods, p. 327–374. *In* J. F. Caddy [ed.] Marine invertebrate fisheries: their assessment and management. John Wiley & Sons, New York, NY.

CROCOS, P. J. 1985. Appraisal of some factors relevant to the development of penaeid prawn population reproductive models, p. 159–164. *In* P. C. Rothlisberg, B. J. Hill, and D. J. Staples [ed.] Second Australian national prawn seminar. NPS2, Cleveland, Australia.

FISHER, R. A. 1970. Statistical methods for research workers. 14th ed. Hafner Press, New York, NY.

FOGARTY, M. J., AND J. S. IDOINE. 1988. Application of a yield and egg production model based on size to an offshore American lobster population. Trans. Am. Fish. Soc. 117: 350–362.

FUJINO, Y. 1980. Approximate binomial confidence limits. Biometrika 67: 677–681.

HARTNOLL, R. G. 1985. Growth, sexual maturity and reproductive output, p. 101–128. *In* A. M. Wenner [ed.] Crustacean issues 3: factors in adult growth. A. A. Balkema, Boston, MA.

KENDALL, M. G., AND A. STUART. 1973. The advanced theory of statistics. Vol. 2. 3rd ed. Griffin, London.

NELDER, J. A., AND R. MEAD. 1965. A simplex method for function minimization. Comput. J. 7: 308–313.

POLOVINA, J. J. 1989. Density dependence in spiny lobster, *Panulirus marginatus*, in the Northwestern Hawaiian Islands. Can. J. Fish. Aquat. Sci. 46: 660–665.

PRESS, W. H., B. P. FLANNERY, S. A. TEUKOLSKY, AND W. T. VETTERLING. 1987. Numerical recipes. The art of scientific computing. Cambridge University Press, New York, NY.

RATKOWSKY, D. A. 1983. Nonlinear regression modeling. Marcel Dekker, New York, NY.

SASTRY, A. N. 1983. Reproduction, p. 179–270. *In* D. E. Bliss [ed.] The biology of Crustacea. Vol. 8. Environmental adaptations. Academic Press, New York, NY.

SCHNUTE, J. T., AND L. J. RICHARDS. 1990. A unified approach to the analysis of fish growth, maturity, and survivorship data. Can. J. Fish. Aquat. Sci. 47: 24–40.

SEBER, G. A. F., AND C. J. WILD. 1989. Nonlinear regression. Wiley, New York, NY.

TUMA, D. J. 1967. A description of the development of primary and secondary sexual characteristics in the banana prawn *Penaeus merguinensis* de Man (Crustacea: Penaeidae). Aust. J. Mar. Freshwater Res. 18: 73–88.

WELCH, D. W., AND R. P. FOUCHER. 1988. A maximum likelihood methodology for estimating length-at-maturity with application to Pacific cod (*Gadus macrocephalus*) population dynamics. Can. J. Fish. Aquat. Sci. 45: 333–343.

WENNER, A. M., C. FUSARO, AND A. OATEN. 1974. Size at onset of sexual maturity and growth rate in crustacean populations. Can. J. Zool. 52: 1095–1106.

WENNER, A. M., H. M. PAGE, AND P. R. SIEGEL. 1985. Variation in size at onset of egg production, p. 149–164. *In* A. M. Wenner [ed.] Crustacean issues 3: factors in adult growth. A. A. Balkema, Boston, MA.

Natural Hybridization between Arctic Char (*Salvelinus alpinus*) and Brook Trout (*S. fontinalis*): Evidence from Northern Labrador

Johan Hammar,[1] J. Brian Dempson, and Eric Verspoor[2]

Department of Fisheries and Oceans, Science Branch, P.O. Box 5667, St. John's, Nfld. A1C 5X1, Canada

Hammar, J., J. B. Dempson, and E. Verspoor. 1991. Natural hybridization between Arctic char (*Salvelinus alpinus*) and brook trout (*S. fontinalis*): evidence from northern Labrador. Can. J. Fish. Aquat. Sci. 48: 1437–1445.

Electrophoretic analysis of successive samples of *Salvelinus* collected in the Fraser River watershed of northern Labrador in 1984 and 1986 revealed the existence of natural hybrids between Arctic char (*Salvelinus alpinus*) and brook trout (*S. fontinalis*). We examined 11 electrophoretic loci in liver tissue; 10 loci were informative and six were diagnostic of the two species and their hybrids. The electrophoretic phenotypes of some hybrid specimens sugested that they were second-generation hybrids and/or backcrosses to the parental species. Hybrids were represented by six different year classes, indicating that crossing between the species in the system is a regular occurrence. The hybrids, although visually difficult to distinguish from brook trout, were meristically intermediate or more closely resembled Arctic char. The observations raise a number of questions regarding the ecological circumstances promoting hybridization in the evolution of Arctic char and brook trout populations. The results stress the need for restrictions on introducing brook trout into systems with original populations of Arctic char. Further, Arctic char from the Fraser River are commonly used for aquaculture research and development; therefore, there is a clear need to screen fish carefully to determine whether or not they represent introgressed gene pools.

Des analyses par électrophorèse d'échantillons successifs de *Salvelinus* recueillis dans le bassin de la rivière Fraser dans le nord du Labrador en 1984 et 1986 ont révélé l'existence d'hybrides naturels de l'omble de l'Arctique (*Salvelinus alpinus*) et la truite mouchetée (*S. fontinalis*). Nous avons examiné 11 locus électrophorétiques dans les tissus du foie; 10 de ces locus ont fourni des informations, et six ont permis d'identifier les deux espèces et leurs hybrides. Les phénotypes électrophériques de certains spécimens hybrides ont suggéré qu'il s'agissait d'hybrides de la deuxième génération, et(ou) de croisements à rebours avec les espèces parentales. Les hybrides étaient représentées par six différentes catégories d'années, ce qui indique que le croisement entre les espèces dans un système survient de façon régulière. Les hybrides, bien que visuellement difficiles à différencier de la truite mouchetée, étaient méristiquement intermédiaires ou ressemblaient plus à l'omble de l'Arctique. Ces observations soulèvent un certain nombre de questions concernant les circonstances écologiques favorisant l'hybridation dans le cadre de l'évolution des populations d'ombles de l'Arctique et de truites mouchetées. Les résultats soulignent la nécessité de restreindre l'introduction de truites mouchetées dans les réseaux comportant des populations originales d'ombles de l'Arctique. En outre, on utilise communément l'omble de l'Arctique de la rivière Fraser pour la recherche et le développement en aquiculture; par conséquent, il est nécessaire de sélectionner avec soin les poissons afin de déterminer s'ils comportent ou non des pools génétiques modifiés par intogression.

Received May 1, 1990
Accepted February 20, 1991
(JA561)

Reçu le 1 mai 1990
Accepté le 20 février 1991

Hubbs (1955) argued that natural hybridization between freshwater fish species in deglaciated holarctic regions should be more common than farther south where species have been endemic for much longer periods. As yet, however, there is little information on natural hybridization among salmonid species, the predominant fish group in arctic and subarctic regions, and little is known of its significance in the evolution of salmonid populations. Where it has been examined, interspecific hybridization has been found to occur, usually between congeneric salmonids. Most commonly, hybridization has occurred where one of the two species involved is introduced (Hubbs 1955; Suzuki and Kato 1966; Svärdson 1979; Campton and Utter 1985; Verspoor 1988), where the environment has been physically or biologically disturbed (Garcia de Leaniz and Verspoor 1989), or where one of the species occurs on the border of its natural ecological distribution (Hammar et al. 1989). As Hubbs (1955) predicted, it appears that hybrids are less frequent where species have evolved together in sympatry over long periods of time.

Described here are repeated observations on natural hybridization between Arctic char (*Salvelinus alpinus*) and brook trout (*S. fontinalis*) in the Fraser River, Labrador. The paper documents electrophoretic evidence of hybridization and backcross-

[1]Present address: Institute of Freshwater Research, S-170, 11 Drottningholm, Sweden and Department of Zoology, Section of Animal Ecology, Uppsala University, Uppsala, Sweden.

[2]Present address: Marine Laboratory, P.O. Box 101, Aberdeen AB9 8D8, Scotland.

ing and examines the meristic intermediacy of the hybrids. The significance of the observations in relation to ecological and management implications is also discussed.

Materials and Methods

Study Area and Samples

The Fraser River is located west of the village of Nain (56°39′N, 63°10′W) on the north Labrador coast (Fig. 1). It is 116 km long with a drainage area of over 1600 km^2. The river flows easterly from the Quebec–Labrador border for 65 km and then drains into Tasisuak Lake before flowing an additional 15 km into Nain Bay. In addition to Arctic char, the river system also contains brook trout, lake trout (*S. namaycush*), threespine and ninespine stickleback (*Gasterosteus aculeatus* and *Pungitius pungitius*), mottled and slimy sculpin (*Cottus bairdi* and *C. cognatus*), and round whitefish (*Prosopium cylindraceum*) (Black et al. 1986).

Four successive samples of *Salvelinus* spp. were examined from the Fraser River. Two anadromous (455–507 mm fork length) and eight small resident char (77–130 mm fork length) were collected on August 1, 1984, in Tasisuak Lake with experimental gill nets (Sample 1). An additional sample of 27 small *Salvelinus* (121–221 mm fork length) was collected by seine net on October 16, 1984, from a semiisolated side channel adjacent to the main river in the principal section used for spawning by anadromous Arctic char (Sample 2). On the same day, another 27 anadromous Arctic char (420–600 mm fork length) (Sample 3) were collected by 114-mm-mesh gill net from the main course of the river for eggs and milt to be used to establish hatchery strains for aquaculture research. A further sample of 43 small *Salvelinus* (156–291 mm fork length) (Sample 4) was collected by seine net on October 16, 1986, from the same location as Sample 2. Samples 1 and 2 were initially collected for electrophoretic screening of the Fraser River stock of Arctic char. The fish in Sample 3 were caught for other purposes and thus were only screened for diagnostic loci. The additional Sample 4 was collected to increase the information on the hybrid frequency. All the fish were packed on ice, transported to the laboratory, and stored frozen at approximately −20°C until analyses were carried out.

Analyses

The fish, with the exception of the sample of anadromous adults, were measured for fork length and weight, and sex and state of maturity were recorded. Otoliths were extracted for age determination according to criteria given by Nordeng (1961).

Electrophoresis was carried out on liver tissue homogenized in 0.025 M mercaptoethanol and in Samples 1 and 2 and the zymograms for seven enzymes, representing 11 loci, were examined (Table 1). Samples 3 and 4 were only examined for four diagnostic loci. The analyses were carried out using horizontal starch-gel electrophoresis with 11% gels (Connaught Starch) and two buffer systems: (A) pH 8.1/8.5 (Ridgeway et al. 1970) and (B) pH 6.0/6.1 (Clayton and Tretiak 1972) (Table 1). A potential of 300 V/cm was applied for 3 h. Stand-

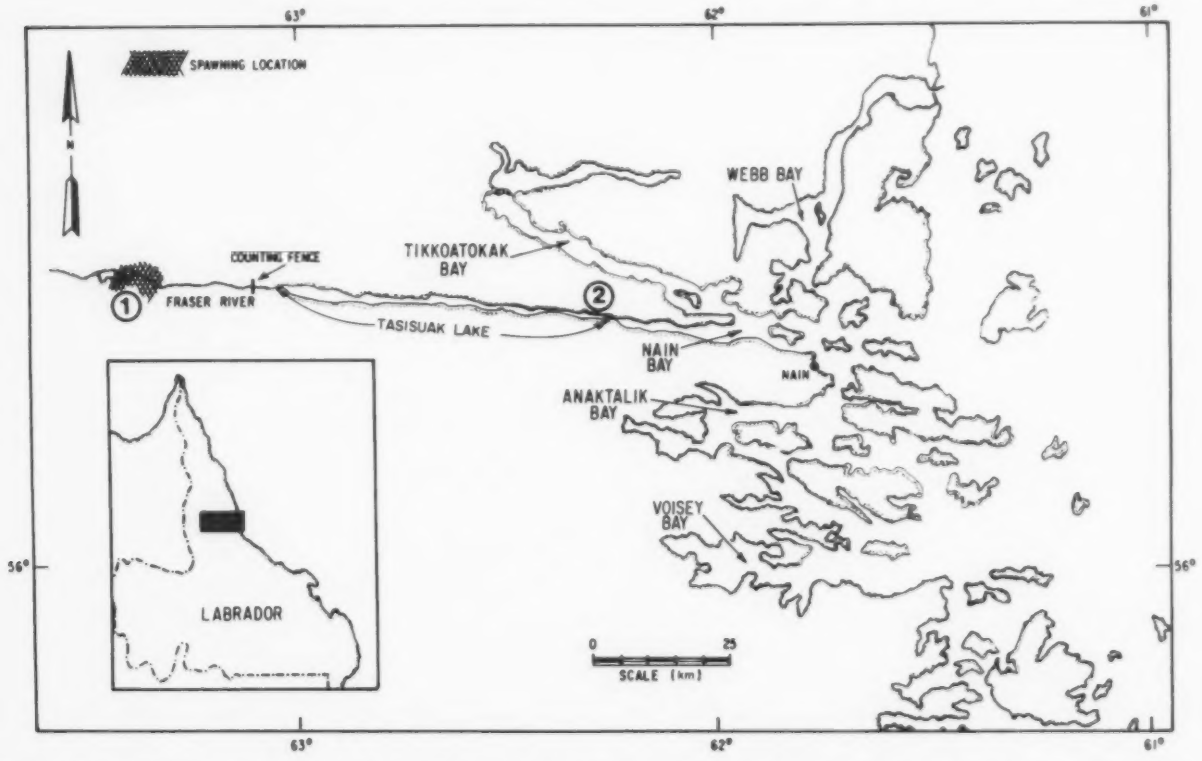


FIG. 1. Map showing the location of the Fraser River, Labrador, and the sites where samples of *Salvelinus* specimens were taken in the watershed. 1 = Fraser River spawning grounds (Samples 1, 2, and 4); 2 = Tasisuak Lake (Sample 3).

TABLE 1. Enzymes, buffer systems, and numbers of loci used from liver tissues analyzed electrophoretically in *Salvelinus* specimens from the Fraser River, Labrador.

Enzyme	Abbreviation	Enzyme No.	Buffer system[a]	Number of loci examined
Alcohol dehydrogenase	ADH	1.1.1.1	A	1
Esterase	EST	3.1.1.-	A	2
Isocitrate dehydrogenase	IDH	1.1.1.42	B	2
Lactate dehydrogenase	LDH	1.1.1.27	A	1
Malate dehydrogenase	MDH	1.1.1.37	B	2
Sorbitol dehydrogenase	SDH	1.1.1.14	A	2
Superoxide dismutase	SOD	1.15.1.1	A	1

[a]See text for details.

ard stains were used for the enzymes (Nyman 1967; Harris and Hopkinson 1976; Allendorf et al. 1977), with stains for IDH, LDH, and MDH employing agar overlays.

The nomenclature employed for describing the electrophoretic loci and alleles follows Shaklee et al. (1989). The identification of the Arctic char loci follows a combination of previous studies on the intraspecific protein variation (Kornfield et al. 1981; Andersson et al. 1983; Johnson 1984). The electrophoretic variants expressed for the brook trout protein loci have also been described previously (Nyman 1967; Morrison 1970; May et al. 1979; McGlade and MacCrimmon 1979; Clayton and Ihssen 1980; Kornfield et al. 1981; Stoneking et al. 1981; Johnson 1984). The common allele was assigned a standard mobility of 100 for both species when this allele was identical in both, but otherwise the 100 allele was assigned to the most common allele in the Arctic char.

Specimens from Samples 2 and 4 only were analyzed for meristic characteristics. The meristic counts were made according to Hubbs and Lagler (1970) and have been recorded previously for Labrador Arctic char by Dempson and Misra (1984) and Dempson (1984, 1985). The first gill arch on the left side of the fish was removed and stained with alizarin red. Gill rakers, including rudiments, were counted under a binocular microscope. Vertebrae and fin ray counts were determined from radiographs. All vertebral centra were counted including those articulating with the fourth and fifth hypurals but excluding the urostyle, as illustrated by Vladykov (1954). Pyloric caecae were counted as they were detached from the stomach. Fish were subsequently divided into groups on the basis of electrophoretic identity, and distributions of meristic counts were then tested for significant differences between groups using a Wilcoxon two-sample test (Sokal and Rohlf 1969). Canonical variates analysis on rank-transformed meristic data (Conover and Iman 1982) was used to quantify the relationships between the two species and their hybrids. Only those characters that were significantly different in the univariate analyses were used.

Results

External Appearance

The 27 small fish caught in the side channel of the Fraser River in 1984 (Sample 2) were initially separated in the laboratory into six "Arctic char" and 21 "brook trout" based on their external appearance. The "Arctic char" were characterized by a paler body without bright yellow and/or red spots whereas the body colour of the "brook trout" was more intense with very distinct red spots, and fins were also red. The dorsal fins of the "Arctic char" were unpatterned and caudal fins were deeply forked. In contrast, the "brook trout" were characterized by clearly vermiculated dorsal fins whereas caudal fins had much less pronounced forks, characters normally associated with *S. fontinalis* (Scott and Crossman 1973). All specimens from Samples 1 and 3 were considered to be Arctic char whereas specimens from Sample 4 were initially thought to be brook trout.

Electrophoretic Patterns

Identification of *S. alpinus* and the hybrids was based on diagnostic phenotypic variation at the *LDH-3**, *MDH-1,2**, *SDH-1,2**, and *SOD** loci (Fig. 2; Table 2). The fast alleles in *LDH-3**, *MDH-1,2**, and *SOD** and the slow allele in *SDH-1,2** were considered specific for *S. alpinus* whereas the alternative alleles were considered specific for *S. fontinalis*. Nondiagnostic variation was also present at the *ADH**, *EST-2**, and *IDH-3,4** loci (Fig. 2; Table 2) whereas the *EST-1** locus was invariant.

In Sample 1, two of the resident specimens caught in Tasisuak Lake showed intermediate phenotypes for the *SDH-1,2** loci whereas alleles at the other loci were characteristic of Arctic char. The other eight specimens were considered pure *S. alpinus*.

With respect to Sample 2, the electrophoretic analysis confirmed the six "Arctic char" to be *S. alpinus*, but the 21 "brook trout" were clearly *S. alpinus* × *S. fontinalis* hybrids. One hybrid specimen expressed homozygous phenotypes for the trout allele of the *LDH-3** locus and the *SDH-1,2** locus whereas the phenotypes for *MDH-1,2** and *SOD** were those of a true hybrid. This strongly suggests and is fully consistent with an individual derived from a backcross of a hybrid with a brook trout. A further three hybrids expressed asymmetric phenotypes differing from a true heterozygote pattern expected in F1 for *SDH-1,2**. This could also result from hybridization beyond the first generation. None of the fish were pure *S. fontinalis* (Table 2).

Specimens from the last two samples (3 and 4) were examined only for the diagnostic *LDH**, *SDH**, and *SOD** loci. All fish in Sample 3 were homozygous for the *LDH*100*, *SOD*100*, and *SDH*100* alleles, confirming these fish to be *S. alpinus*. Thirty-seven specimens of Sample 4 were homozygous for *LDH*35*, *SOD*55*, and *SDH*160* alleles. This was opposite to that observed in Arctic char specimens in Samples 1, 2, and 3 and confirmed that these fish were *S. fontinalis*. The other six specimens had intermediate phenotypes for these loci (Table 2), consistent with their being true hybrids.

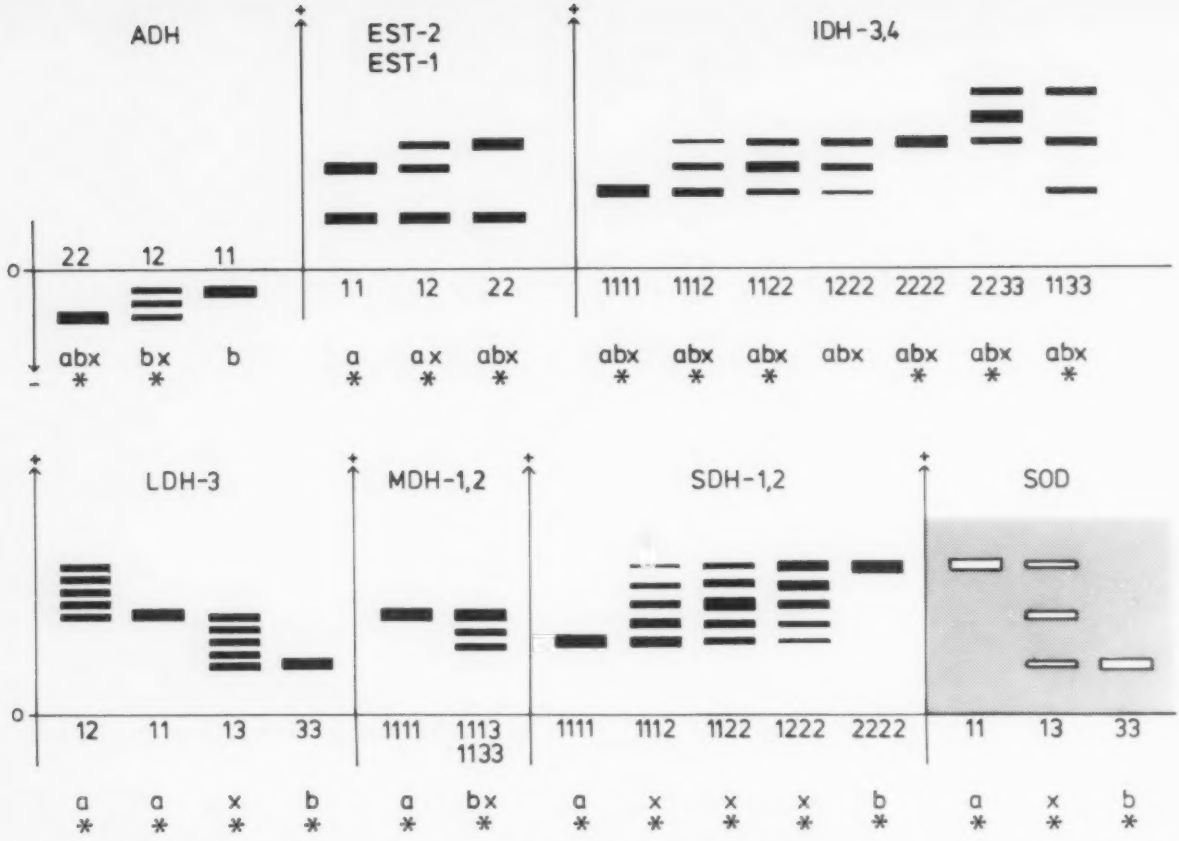


FIG. 2. Electrophoretic phenotypes observed at loci found to be variable in the *Salvelinus* specimens from the Fraser River, Labrador. The proposed genetic interpretations, specific species markers (a = Arctic char, b = brook trout, × = hybrid) used, and the recorded phenotypes (*) are given below each zymogram.

Meristic Characters

The distribution of meristic characters for Arctic char and brook trout generally overlap, making detection of hybrids using single meristic traits difficult. Analysis of the meristic traits of the 27 specimens of Sample 2, independent of their characterization based on external appearance or protein phenotypes, initially suggested that all specimens belonged to one species, Arctic char. The values obtained were all within the normal range of variation exhibited by the species (Scott and Crossman 1973) although slightly lower than that previously reported for Arctic char in this region (Dempson and Misra 1984). After separation of the fish based on electrophoretic characteristics, it was clear that the "brook trout" looking specimens had some meristic counts distinct from those of the "Arctic char."

The meristic characters for the Arctic char, brook trout, and hybrids identified in Samples 2 and 4 are summarized in Table 3. Wilcoxon two-sample tests indicated significant differences, relating to the distribution of the number of vertebrae and gill rakers, among the three groups. For four of the characters (anal and pelvic fin rays, branchiostegals, and pyloric caeca) the distributions were not significantly different between the hybrids and either of the parental species. The brook trout had significantly lower distributions of dorsal and pectoral fin rays, vertebrae, and gill rakers in comparison with hybrid specimens. In contrast, Arctic char had significantly higher distributions of vertebrae and both lower and total gill raker counts than the hybrids. Considered collectively, the distributions of the traits in the hybrids suggest a closer affinity with the Arctic char than with the brook trout.

The first canonical variate separated the brook trout from both the hybrids and Arctic char (Fig. 3). Numbers of vertebrae and lower gill rakers are the two most important characters in the first canonical variate contributing 53.0 and 36.1% of the weight respectively to this function. Numbers of both characters increase from left to right along the first axis. The second canonical variate separated the hybrids from the Arctic char. In this function, numbers of upper gill rakers (27.3%), pectoral fin rays (25.8%), and lower gill rakers (21.6%) were the most important characters. Upper gill rakers and pectoral fin rays increased positively on the axis whereas the lower gill rakers decreased.

Ecological Characteristics

Hybrid specimens identified from Fraser River Samples 2 and 4 ranged in age from 2 to 8 yr (121–291 mm) representing six year-classes from 1976 to 1982. The Arctic char specimens were age 3 and 4 yr (131–161 mm) whereas brook trout varied

TABLE 2. Phenotypes observed at the various liver enzyme loci in the *Salvelinus* specimens from the Fraser River and Tasisuak Lake, Labrador. Species designations: A = Arctic char, B = brook trout, X = hybrid (n.e. = not examined).

Locus/phenotype	Species designation	Sample 1 Tasisuak Lake, 1984		Sample 2 Fraser River, 1984		Sample 3 Fraser River, 1984	Sample 4 Fraser River, 1986	
		Anadromous char (N = 2)	Resident char (N = 8)	Resident char (N = 6)	Hybrids (N = 21)	Anadromous char (N = 27)	Hybrids (N = 6)	Brook trout (N = 37)
*ADH**						n.e.	n.e.	n.e.
(-25/-100)	B				3			
(-100/-100)	A,B	2	8	6	18			
*EST-1**						n.e.	n.e.	n.e.
(100/100)	A,B	2	8	6	21			
*EST-2**						n.e.	n.e.	n.e.
(90/90)	A	1	1					
(90/100)	A		3	2				
(100/100)	A,B	1	4	4	21			
*IDH-3,4**						n.e.	n.e.	n.e.
(85/85/85/85)	A,B		1					
(85/85/85/100)	A,B	1	3	2				
(85/85/100/100)	A,B	1	3	2	2			
(100/100/100/100)	A,B		1	2	2			
(100/100/115/115)	A,B				5			
(85/85/115/115)	A,B				12			
*LDH-3**								
(35/35)	B				1			37
(35/100)	×				20		6	
(100/100)	A	2	7	6		27		
(100/130)	A		1					
*MDH-1,2**						n.e.	n.e.	n.e.
(70/70/100/100)	×				21			
(70/100/100/100)	×				21			
(100/100/100/100)	A	2	8	6				
*SDH-1,2**								
(100/100/100/100)	A	2	6	6		27		
(100/100/100/160)	×				2			
(100/100/160/160)	×		2		17		6	
(100/160/160/160)	×				1			
(160/160/160/160)	B				1			37
*SOD**								
(55/55)	B							37
(55/100)	×				21		6	
(100/100)	A	2	8	6		27		

TABLE 3. Means and minimum–maximum values of meristic traits counted in electrophoretically identified Arctic char, brook trout, and hybrid specimens collected from the Fraser River and Tasisuak Lake, 1984 and 1986 (Samples 2 and 4), and results of Wilcoxon two-sample tests. Significance levels: $^{*}P < 0.05$; $^{**}P < 0.01$.

Meristic character	Arctic char (1)			Hybrid (2)			Brook trout (3)			*Wilcoxon two-sample test*		
										1 vs. 2	1 vs. 3	2 vs. 3
	N	Mean	Min–max	N	Mean	Min–max	N	Mean	Min–max	$\|Z\|$	$\|Z\|$	$\|Z\|$
Dorsal fin	6	14.7	13–16	27	14.2	13–15	37	13.9	13–15	1.36	2.20*	2.08**
Anal fin	6	12.8	11–14	27	13.0	12–15	37	12.9	12–15	0.16	0.0	0.51
Pectoral fin	6	13.3	12–14	27	13.9	13–15	29	12.8	12–14	1.33	1.73	4.78**
Pelvic fin	6	9.0	9	25	8.8	8–10	33	8.6	8–9	1.15	1.94	1.27
Vertebrae	6	65.2	63–66	27	62.9	60–65	37	59.3	58–61	3.19**	4.10**	6.82**
Upper gill raker	6	9.7	9–10	26	9.6	7–11	36	7.3	5–10	0.03	3.24**	5.32**
Lower gill raker	6	14.8	13–16	26	13.4	12–15	36	11.1	9–13	2.83**	3.98**	6.16**
Total gill raker	6	24.5	23–26	26	23.0	19–26	36	18.4	14–23	2.19*	3.88**	6.06**
Branchiostegals	6	10.8	10–12	26	11.2	10–13	37	11.1	9–13	1.06	0.92	0.61
Pyloric caeca	6	36.5	33–41	25	41.8	31–57	33	42.3	34–53	1.93	2.11*	0.31
Fork length (mm)	6	147	131–161	27	170	121–291	37	207	156–271			
Age (yr)	6	3.7	3–4	27	3.7	2–8	33	5.3	4–9			

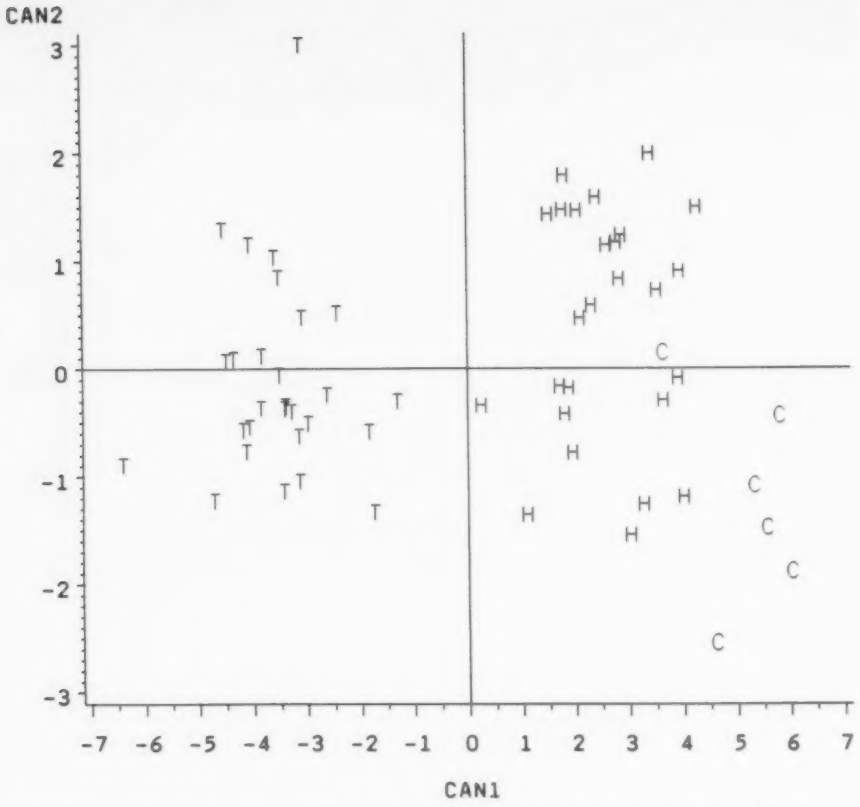


FIG. 3. Plot of the first two canonical variables from an analysis of meristic characters of Arctic char (C), brook trout (T), and their hybrids (H) from the Fraser River, Labrador.

in age and fork length from 4 to 9 yr and 156 to 271 mm, respectively (Table 3). All specimens from Sample 2 were sexually mature and the sex ratio showed an excess of males. All of the fish from Sample 4 collected in 1986 were also sexually mature. The proportions of males among the brook trout and hybrids were 67 and 19%, respectively.

Discussion

The observations reported in this paper represent the first documented case of natural hybridization between Arctic char and brook trout. Although some authors have suggested this to occur (Vladykov 1954; Alm 1955; Wooding 1959), reviews of the literature revealed no previous reports of natural hybridization between the two species (Slastenenko 1957; Behnke 1972; Schwartz 1972, 1981; Dangel et al. 1973; Marshall 1977, 1981; Chevassus 1979; Marshall and Layton 1985). This may have been expected given the similarity in general appearance of the hybrid with one of the two parental species. With 27 of 70 small-sized fish (39%) (Samples 2 and 4) positively identified as hybrids and backcrosses, and representing six different year-classes, the observations from the Fraser River, Labrador, suggest that hybridization may be a common occurrence in areas where the ranges of the two species overlap naturally. The two species are known to produce fertile and viable hybrids under artificial conditions (Schindler 1938; Alm 1955; Suzuki 1974; Chevassus 1979). Nevertheless, Nei's genetic distance between the species is 0.36, the same as between Atlantic salmon (*Salmo salar*) and brown trout (*S. trutta*) (Johnson 1984) where hybridization is widespread (e.g. Verspoor 1988; Garcia de Leaniz and Verspoor 1989). Also, in common with Atlantic salmon and brown trout, their chromosome numbers differ (Arctic char $2N = 80$; brook trout $2N = 84$), although they have the same number of chromosome arms (100) (Hartley 1987).

A variety of general ecological mechanisms could influence the incidence of natural hybridization among northern salmonids. For example, the ecological plasticity of Arctic char has resulted in a combination of life history strategies and tactics that enables the species complex to survive in most cool oligotrophic habitats (Skreslet 1973; Johnson 1980, 1983; Barbour 1984; Hammar 1989). In northern allopatric situations, Arctic char utilize a far wider niche in contrast with areas farther south where they coexist in more narrow niches with both vertebrate and invertebrate competitors (Filipsson and Svärdson 1976; Hammar 1987; Svärdson et al. 1988). According to Savvaitova (1985), this is a general characteristic for northern fish and suggests that hyrid zones (defined by Barton and Hewitt 1985) in northern areas tend to represent borderlines between species with much broader ecological frames than in the south. Thus, higher incidences of *Salvelinus* hybrids in regions would be expected where exploratory individuals of brook trout or lake trout advance farther north into established Arctic char territory (Hammar 1989), circumstances analogous to species

introductions which, according to Hubbs (1955), is an important factor believed to contribute to hybridization.

Disparity in parental population sizes is another reason suggested to explain the occurrence of natural hybridization (Hubbs 1955; Suzuki and Kato 1966; Greenfield and Greenfield 1972; Rakocinski 1980; Whitmore 1983; Hammar et al. 1989). In the Fraser River, anadromous Arctic char appear to be the most abundant species (Dempson and Green 1985). During 5 yr of investigations more than 15 000 char were counted migrating upstream through a fish-counting fence. In contrast, only 62 brook trout passed upstream and 89 were counted moving downstream. This suggests that brook trout may be scarce relative to the Arctic char population and favour the occurrence of hybridization.

The common occurrence of natural hybridization between Arctic char and brook trout in Fraser River may also imply a periodic breakdown in reproductive isolating mechanisms of the two species. Both species in the Fraser River are sympatric while breeding, have overlapping spawning periods (Dempson and Green 1985), and display similar spawning behaviour (Johnson 1980; Power 1980). In the semiisolated side channels where hybrid specimens were collected, fish were frequently crowded. This has been observed on at least five other occasions (years) when Arctic char were collected for broodstock removal. Occasionally, in years of low water levels during the fall, these side channels can be completely isolated from the main stem of the river as observed in 1984. Any accidental "landlocking" of mature anadromous Arctic char with resident brook trout in these pools could contribute to the potential incidence of hybridization.

Most of the morphological and meristic characters of Arctic char and brook trout overlap (Scott and Crossman 1973), and in areas where the two species coexist, potential difficulties in distinguishing the two species have been noted (Behnke 1972). McGlade and MacCrimmon (1979) reported several meristic characters for brook trout in the province of Quebec with values higher than previously known for the species, making them similar to Arctic char, and they suggested that electrophoretic methods might be needed for positive identification where the two species coexist. Fraser River hybrids had mean meristic values between those of the Arctic char and brook trout for six of 10 characters examined. Multivariate statistical analyses suggested a closer affinity to Arctic char than to brook trout and separated out the hybrids following positive electrophoretic identification.

Since Nyman (1965, 1967) first showed that artificial hybrids between Arctic char and brook trout can be unequivocally identified using protein electrophoresis, a number of diagnostic tissue protein loci have been identified. The electrophoretic banding patterns of the four proteins used to identify hybrids in this study (*LDH-3**, *MDH-1,2**, *SDH-1,2**, and *SOD**) have been described previously for Arctic char and/or brook trout and their hybrid by Honsig-Erlenburg (1982) and Johnson (1984). While other loci such as *ADH**, *EST-2**, and *IDH-3,4** may also be diagnostic in certain situations, they are not likely to be useful for *Salvelinus* specimens in Labrador where the Arctic char and brook trout share common alleles at these loci (this study, J. Hammar and E. Verspoor, unpubl. data). In general, the *SOD** and *SDH-1,2** loci would offer the best test for F1 hybrids, as they are both present in the liver and can be stained for on a single starch-gel slice.

Sorbitol dehydrogenase (SDH) expressed in the liver has been described as a tetrameric enzyme encoded by two loci in *Salmo* (Engel et al. 1970) but only by a single locus in brook trout, lake trout, and Arctic char (May et al. 1979; Ferguson 1981; Stoneking et al. 1981; Andersson et al. 1983; Johnson 1984; Hindar et al. 1986). In Fraser River hybrids, electrophoretic variation observed for this enzyme was consistent with a duplicated locus with five phenotypes (Fig. 2). We have, therefore, attributed variation in this enzyme to expression of two comigrating, duplicated loci. The question of how many SDH loci are expressed in the species can only be resolved by breeding studies.

The electrophoretic patterns also give evidence of hybridization beyond the F1 generation. Three specimens of the 21 individuals expressing hybrid phenotypes in Sample 2 showed electrophoretic patterns which could arise in individuals derived from crosses involving hybrids. One individual would appear more specifically to be the result of backcrossing of a hybrid into the trout populations. With the data available, it is, however, difficult to determine the extent of gene flow that may occur between Arctic char and brook trout populations. In two specimens of lake resident char from Sample 1, evidence of trout alleles expressed by the *SDH** loci was found. Since an allele electrophoretically equivalent to the brook trout *SDH** allele has not been reported in Arctic char populations from North America (Kornfield et al. 1981; Johnson 1984; Hammar et al. 1989; J. Hammar and E. Verspoor, unpubl. data), it is conceivable that its presence in char populations in the Fraser River is the result of hybridization with brook trout. If so, this would be a case of introgression. Alternatively, it is a remote possibility that the allele in question also occurs in Arctic char but is rare and that the lack of observation of it is due to a limited number of specimens examined.

Our observations on natural hyridization between Arctic char and brook trout in Labrador raise a number of questions regarding its consequences for the reproductive isolating mechanisms and speciation processes in *Salvelinus* in North America. Progenies of interspecific hybrids generally suffer from reduced viability or fertility, assumed to result from the breaking up of coadapted loci combinations that enhance each other's phenotypic value (Hedrick 1985), giving reduced fitness in hybrids. However, in hybrid zones, where the frontier is determined by a physical environmental limitation such as low temperature, preferences for temperature in *Salvelinus* hybrids may be intermediate to that of the parental species, as shown experimentally (Peterson et al. 1979). Repeated hybridization and/or backcrosses may thus add characters desirable for survival further north, from the char genome into the trout genome. In Labrador, this would mean higher levels of heterozygosity in Arctic char populations and a larger proportion of shared variant alleles with brook trout than in, for example, north European regions. Preliminary studies show that this may actually be the case (Hammar 1989; Hammar et al. 1989; this study; J. Hammar and E. Verspoor, unpubl. data), and similar findings for cyprinids have been reported elsewhere (Rakocinski 1980).

Management Implications

Common occurrence of natural hybridization has implications for the introduction of brook trout into Arctic char lakes in other regions. Original gene pools may be altered by introductions of closedly related species which hybridize with the local ones (Naevdal and Dalpadado 1986). Numerous introductions of brook trout have been performed all over the world, and populations have become naturalized in systems containing

other salmonids, such as Arctic char (MacCrimmon and Campbell 1969). So far, only suspected hybridization with Arctic char has been reported, but the present results stress the need to consider further stockings in light of preserving the genetic identity of existing populations.

In recent years, wild Arctic char from the Fraser River, Labrador, have frequently been used as a brood source for Federal and Canadian Provincial hatcheries in Newfoundland, New Brunswick, and Manitoba. Progeny from these fish have also been used in various aquaculture and related experiments (Baker 1983; Papst and Hopky 1983; Eales and Shostak 1985, 1986; Jones et al. 1985, 1987; Delabbio and Glebe 1987; Fletcher et al. 1988; and references in de March and Baker 1990). Ironically, the Arctic char from the Fraser River were thoroughly analyzed for pathogenic disease organisms as a requisite for the transfer of fish according to the Canadian Fish Health Protection Regulations (Canada Department of Fisheries and Oceans 1984). To date, no such requirement is in place with respect to the genetic screening of fish populations.

Acknowledgments

The authors wish to thank Larry LeDrew and Eva Sköld for help with the collection of samples from Tasisuak Lake in 1984, and personnel from the Department of Fisheries, Province of Newfoundland, for assistance in collecting fish from the Fraser River in 1986. We also thank Erik Degerman, John Gibson, Michael O'Connell, Lennart Nyman, Rex Porter, James Reist, Gunnar Svärdson, and an anonymous referee for reviewing earlier drafts of the manuscript. Steve Dawson, George Furey, Larry LeDrew, and Eva Sköld assisted with sampling and meristic analyses in the laboratory.

References

ALLENDORF, F. W., N. MITCHELL, N. RYMAN, AND G. STÅHL. 1977. Isozyme loci in brown trout (*Salmo trutta* L.): detection and interpretation from population data. Hereditas 88: 179–190.

ALM, G. 1955. Artificial hybridization between different species of the salmon family. Rep. Inst. Freshwater Res. Drottningholm 36: 13–56.

ANDERSSON, L., N. RYMAN, AND G. STÅHL. 1983. Protein loci in the Arctic charr, *Salvelinus alpinus* L.: electrophoretic expression and genetic variability patterns. J. Fish Biol. 23: 75–94.

BAKER, R. 1983. The efects of temperature, ration and size on the growth of Arctic charr (*Salvelinus alpinus* L.). M.Sc. thesis, University of Manitoba, Winnipeg, Man. 227 p.

BARBOUR, S. E. 1984. Variation in life history, ecology and resource utilization by Arctic charr, *Salvelinus alpinus* (L.) in Scotland. PhD. thesis, University of Edinburgh, Edinburgh, Scotland. 181 p.

BARTON, N. H., AND G. M. HEWITT. 1985. Analysis of hybrid zones. Annu. Rev. Ecol. Syst. 16: 113–148.

BEHNKE, R. J. 1972. The systematics of salmonid fishes of recently glaciated lakes. J. Fish. Res. Board Can. 29: 639–671.

BLACK, G. A., J. B. DEMPSON, AND W. J. BRUCE. 1986. Distribution and postglacial dispersal of freshwater fishes of Labrador. Can. J. Zool. 64: 21–31.

CAMPTON, D. E., AND F. M. UTTER. 1985. Natural hybridization between steelhead trout (*Salmo gairdneri*) and coastal cutthroat trout (*Salmo clarki clarki*) in two Puget Sound streams. Can. J. Fish. Aquat. Sci. 42: 110–119.

CANADA DEPARTMENT OF FISHERIES AND OCEANS. 1984. Fish health protection regulations: manual of compliance. Fish. Mar. Serv. Misc. Spec. Publ. 31 (Revised): 43 p.

CHEVASSUS, B. 1979. Hybridization in salmonids: results and perspectives. Aquaculture 17: 113–128.

CLAYTON, J. W., AND D. N. TRETIAK. 1972. Amine-citrate buffers for pH control in starch gel electrophoresis. J. Fish. Res. Board Can. 29: 1169–1172.

CLAYTON, J. W., AND P. E. IHSSEN. 1980. Dehydrogenase isozymes in *Salvelinus*: genetics and interspecies phenotypic comparisons, p. 339–356. *In* E. K. Balon [ed.] Charrs: salmonid fishes of the genus *Salvelinus*. W. Junk Publ., The Hague, The Netherlands.

CANOVER, W. J., AND R. L. IMAN. 1982. The rank transformation in discriminant analysis, p. 681–690. *In* Proc. Seventh Annual Sugi Conference, San Francisco, California. SAS Institute, Cary, NC.

DANGEL, J. R., P. T. MACY, AND F. C. WITHLER. 1973. Annotated bibliography of interspecific hybridization of fishes of the subfamily Salmoninae. NOAA Tech. Memo. NMFS NWFC-1: 48 p.

DELABBIO, J. L., AND B. D. GLEBE. 1987. Comparative saltwater performance of two Canadian Arctic char stocks. Proc. Annu. Meet. Aquacult. Assoc. Can. 1: 44–45.

DE MARCH, B. G. E., AND R. F. BAKER. 1990. Culture history of the first hatchery generation of Arctic charr (*Salvelinus alpinus*) from the Fraser River, Labrador (1980–1987). Can. MS. Rep. Fish. Aquat. Sci. 2084: 11 p.

DEMPSON, J. B. 1984. Identification of anadromous Arctic charr stocks in coastal areas of northern Labrador, p. 143–162. *In* L. Johnson and B. L. Burns [ed.] Biology of the Arctic charr. Proceedings of the International Symposium on Arctic Charr, Winnipeg, Man.

1985. Geographical variation in meristic characteristics of landlocked Arctic charr (*Salvelinus alpinus*) from insular Newfoundland and Labrador, p. 19–28. *In* Proc. Third ISACF Workshop on Arctic Char, 1984. ISACF Inf. Ser. No. 3. Inst. Freshwater Res. Drottningholm.

DEMPSON, J. B., AND J. M. GREEN. 1985. Life history of anadromous Arctic charr, *Salvelinus alpinus*, in the Fraser River, northern Labrador. Can. J. Zool. 63: 315–324.

DEMPSON, J. B., AND R. K. MISRA. 1984. Identification of anadromous Arctic charr (*Salvelinus alpinus*) stocks in coastal areas of northern Labrador based on a multivariate statistical analysis of meristic data. Can. J. Zool. 62: 631–636.

EALES, J. G., AND S. SHOSTAK. 1985. Correlations between food ration, somatic growth parameters and thyroid function in Arctic char, *Salvelinus alpinus* L. Comp. Biochem. Physiol. 80A: 553–558.

1986. Influence of temperature and pH on free T_4 and free T_3 in charr and trout plasma. Gen. Comp. Endocrinol. 61: 272–277.

ENGEL, W., J. OP'T HOF, AND U. WOLF. 1970. Genduplikation durch polyploide evolution: die isoenzxyme der sorbit-dehydrogenase bei heringsund lachsartigen fischen (Isospondyli). Humangenetik 9: 157–163.

FERGUSON, A. 1981. Systematics of Irish charr as indicated by electrophoretic analysis of tissue proteins. Biochem. Syst. Ecol. 9: 225–232.

FILIPSSON, O., AND G. SVÄRDSON. 1976. Principles for the management of char populations. Inf. Inst. Freshwater Res. Drottningholm 2: 79 p. (In Swedish with English summary)

FLETCHER, G. L., M. H. KAO, AND J. B. DEMPSON. 1988. Lethal freezing temperatures of Arctic char and other salmonids in the presence of ice. Aquaculture 71: 369–378.

GARCIA DE LEANIZ, C., AND E. VERSPOOR. 1989. Natural hybridization between Atlantic salmon, *Salmo salar*, and brown trout, *Salmo trutta*, in northern Spain. J. Fish. Biol. 34: 41–46.

GREENFIELD, D. W., AND T. GREENFIELD. 1972. Introgressive hybridization between *Gila orcutti* and *Hesperolecus symmetricus* (Pisces: Cyprinidae) in the Cuyama River basin, California: I. Meristics, morphometrics and breeding. Copeia 1972: 849–859.

HAMMAR, J. 1987. Zoogeographical zonation of fish communities in insular Newfoundland; a preliminary attempt to use Arctic char population ecology to describe early postglacial colonization interactions, p. 31–38. *In* Proc. Fourth ISACF Workshop on Arctic Char, 1986. ISACF Inf. Ser. No. 4. Inst. Freshwater Res. Drottningholm.

1989. Freshwater ecosystems of polar regions: vulnerable resources. Ambio 18: 6–22.

HAMMAR, J., J. B. DEMPSON, AND E. SKÖLD. 1989. Natural hybridization between Arctic char (*Salvelinus alpinus*) and lake char (*S. namaycush*): evidence from northern Labrador. Nord. J. Freshwater Res. 65: 54–70.

HARRIS, H., AND D. A. HOPKINSON. 1976. Handbook of enzyme electrophoresis in human genetics. North-Holland Publ. Co., Amsterdam, The Netherlands.

HARTLEY, S. E. 1987. The chromosomes of salmonid fishes. Biol. Rev. 62: 197–214.

HEDRICK, P. W. 1985. Genetics of populations. Jones and Bartlett, Inc., Boston, MA. 629 p.

HINDAR, K., N. RYMAN, AND G. STÅHL. 1986. Genetic differentiation among local populations and morphotypes of Arctic charr, *Salvelinus alpinus*. Biol. J. Linn. Soc. 27: 269–285.

HONSIG-ERLENBURG, W. 1982. Die identifikation von salmoniden mittels biochemischer merkmale (am beispiel der LDH bei saiblingen). Wissenschaft 35: 14–17.

HUBBS, C. L. 1955. Hybridization between fish species in nature. Syst. Zool. 4: 1–20.

HUBBS, C. L., AND K. F. LAGLER. 1970. Fishes of the Great Lakes region. University of Michigan Press, Ann Arbor, MI. 213 p.

JOHNSON, K. R. 1984. Protein variation in salmoninae: genetic interpretations of electrophoretic banding patterns, linkage associations among loci, and evolutionary relationships among species. Ph.D. thesis, Pennsylvania State University, University Park, PA. 181 p.

JOHNSON, L. 1980. The Arctic charr, *Salvelinus alpinus*, p. 15–98. *In* E. K. Balon [ed.] Charrs: salmonid fishes of the genus *Salvelinus*. W. Junk Publ., The Hague, The Netherlands.

1983. Homeostatic characteristics of single species fish stocks in Arctic lakes. Can. J. Fish. Aquat. Sci. 40: 987–1024.

JONES, K. A., S. B. BROWN, AND T. J. HARA. 1987. Behavioural and biochemical studies of onset and recovery from acid stress in Arctic char (*Salvelinus alpinus*). Can. J. Fish. Aquat. Sci. 44: 373–381.

JONES, K. A., T. J. HARA, AND E. SCHERER. 1985. Behavioural modifications in Arctic char (*Salvelinus alpinus*) chronically exposed to sublethal pH. Physiol. Zool. 58: 400–412.

KORNFIELD, I., K. F. BELAND, J. R. MORING, AND F. W. KIRCHESIS. 1981. Genetic similarity among endemic Arctic char (*Salvelinus alpinus*) and implications for their management. Can. J. Fish. Aquat. Sci. 38: 32–39.

MACCRIMMON, H. R., AND J. S. CAMPBELL. 1969. World distribution of brook trout, *Salvelinus frontinalis*. J. Fish. Res. Board Can. 26: 1699–1725.

MARSHALL, K. E. 1977. A bibliography of the Arctic char, *Salvelinus alpinus* (L.) complex to 1976. Fish. Mar. Serv. Tech. Rep. 621: 49 p.

1981. A bibliography of the Arctic charr, *Salvelinus alpinus* (L.) complex to 1980. Can. Tech. Rep. Fish. Aquat. Sci. 1004: 68 p.

MARSHALL, K. E., AND M. LAYTON. 1985. A bibliography of the Arctic charr, *Salvelinus alpinus* (L.) complex: 1981 through 1984. Can. Tech. Rep. Fish. Aquat. Sci. 1345: 16 p.

MAY, B., J. E. WRIGHT, AND M. STONEKING. 1979. Joint segregation of biochemical loci in Salmonidae: results from experiments with *Salvelinus* and review of the literature on other species. J. Fish. Res. Board Can. 36: 1114–1128.

MCGLADE, J., AND H. MACCRIMMON. 1979. Taxonomic congruence in three populations of Quebec brook trout, *Salvelinus fontinalis* (Mitchill). Can. J. Zool. 57: 1998–2009.

MORRISON, W. J. 1970. Nonrandom segregation of two lactate dehydrogenase subunit loci in trout. Trans. Am. Fish. Soc. 99: 193–206.

NAEVDAL, G., AND P. DALPADADO. 1986. Interspecific hybridization — cold-water species. EIFAC/FAO Symp. R:12. Symposium on selection, hybridization and genetic engineering in aquaculture of fish and shellfish for consumption and stocking. Bordeaux, France, May 1986.

NORDENG, H. 1961. On the biology of char (*Salmo alpinus*) in Salangen, north Norway. I. Age, and spawning frequency determined from scales and otoliths. Nytt Mag. Zool. 10: 67–123.

NYMAN, L. 1965. Variation of proteins in hybrids and parental species of fishes. Rep. Swed. Salmon Res. Inst. No. 13. 11 p.

1967. Protein variation in Salmonidae. Rep. Inst. Freshwater Res. Drottningholm 47: 5–38.

PAPST, M. H., AND G. E. HOPKY. 1983. Growth of Arctic charr (*Salvelinus alpinus* L.) in a pilot commercial rearing system. Can. Tech. Rep. Fish. Aquat. Sci. 1182: 16 p.

PETERSON, R. H., A. M. SUTTERLIN, AND J. L. METCALFE. 1979. Temperature preference of several species of *Salmo* and *Salvelinus* and some of their hybrids. J. Fish. Res. Board Can. 36: 1137–1140.

POWER, G. 1980. The brook charr, *Salvelinus fontinalis*, p. 141–203. *In* E. K. Balon [ed.] Charrs: salmonid fishes of the genus *Salvelinus*. W. Junk Publ., The Hague, The Netherlands.

RAKOCINSKI, C. F. 1980. Hybridization and introgression between *Campostoma oligolepis* and *C. anomalum pullum* (Cypriniformes: Cyprinidae). Copeia 1980: 584–594.

RIDGEWAY, G. J., S. W. SHERBURNE, AND R. D. LEWIS. 1970. Polymorphisms in the esterases of Atlantic herring. Trans. Am. Fish. Soc. 99: 147–151.

SAVVAITOVA, K. A. 1985. Charrs of the *Salvelinus* genus: formation and structure of the population systems, p. 144–156. *In* Proc. Third ISACF Workshop on Arctic Char, 1984. ISACF Inf. Ser. No. 3. Inst. Freshwater Res. Drottningholm.

SCHINDLER, O. 1938. Uber larven und jungfische der Kreuzungen zwischen seesaibling und bachsaibling. Int. Rev. Hydrobiol. 37: 385–404. (In German)

SCHWARTZ, F. J. 1972. World literature to fish hybrids with an analysis by family, species, and hybrid. Gulf Coast Res. Lab. Ocean Springs, MS. Publ. Gulf Coast Res. Lab. Mus. No. 3: 328 p.

1981. World literature to fish hybrids with an analysis by family, species, and hybrid: Supplement 1. NOAA Tech. Rep. NMFS SSRF-750.

SCOTT, W. B., AND E. J. CROSSMAN. 1973. Freshwater fishes of Canada. Bull. Fish. Res. Board Can. 184: 966 p.

SHAKLEE, J. B., F. W. ALLENDORF, D. C. MORIZOT, AND G. S. WHITT. 1989. Genetic nomenclature for protein-coding loci in fish: proposed guidelines. Trans. Am. Fish. Soc. 118: 218–227.

SKRESLET, S. 1973. The ecosystem of the arctic lake Nordlaguna, Jan Mayen Island. III. Ecology of Arctic char, *Salvelinus alpinus* (L.) Astarte 6: 43–54.

SLASTENENKO, E. P. 1957. A list of natural fish hybrids of the world. Hydrobiol. Res. Inst. Fac. Sci. Univ. Istanbul Ser. B 4: 76–97.

SOKAL, R. R., AND F. J. ROHLF. 1969. Biometry. W. H. Freeman and Company, San Francisco, CA. 776 p.

STONEKING, M., D. J. WAGNER, AND A. C. HILDEBRAND. 1981. Genetic evidence suggesting subspecific differences between northern and southern populations of brook trout (*Salvelinus fontinalis*). Copeia 1981: 810–819.

SUZUKI, R. 1974. Inter-crossings and back-crossings of F1 hybrids among salmonid fishes. Bull. Freshwater Fish. Res. Lab. Tokyo 24: 11–31.

SUZUKI, R., AND T. KATO. 1966. Hybridization in nature between salmonid fishes. Bull. Freshwater Fish. Res. Lab. Tokyo 16: 83–90.

SVÄRDSON, G. 1979. Speciation of Scandinavian *Coregonus*. Rep. Inst. Freshwater Res. Drottningholm 57: 95 p.

SVÄRDSON, G., O. FILIPSSON, M. FÜRST, M. HANSON, AND N.-A. NILSSON. 1988. The significance of glacial relicts for the fish fauna of Lake Vättern. Inf. Inst. Freshwater Res. Drottningholm 15: 61 p. (In Swedish with English summary)

VERSPOOR, E. 1988. Widespread hybridization between native Atlantic salmon, *Salmo salar*, and introduced brown trout, *S. trutta*, in eastern Newfoundland. J. Fish. Biol. 32: 327–334.

VLADYKOV, V. D. 1954. Taxonomic characters of the eastern North American chars (*Salvelinus* and *Cristivomer*). J. Fish. Res. Board Can. 11: 904–932.

WHITMORE, D. H. 1983. Introgressive hybridization of smallmouth bass (*Micropterus dolomieui*) and Guadalupe bass (*M. treculi*). Copeia 1983: 672–679.

WOODING, F. H. 1959. The book of Canadian fishes. McGraw-Hill Ryerson Ltd., Toronto, Ont. 303 p.

Comparison of Methods Used to Estimate Age and Length of Fishes at Sexual Maturity Using Populations of White Sucker (*Catostomus commersoni*)

Edward A. Trippel[1] and Harold H. Harvey

Department of Zoology, University of Toronto, Toronto, Ont. M5S 1A1, Canada

Trippel, E. A., and H. H. Harvey. 1991. Comparison of methods used to estimate age and length of fishes at sexual maturity using populations of white sucker (*Catostomus commersoni*). Can. J. Fish. Aquat. Sci. 48: 1446–1459.

We compared six methods of estimating age and length at sexual maturity of iteroparous fishes: probit analysis, maximum likelihood methodology, linear regression on arcsine - square root transformed data, Lysack's formula, visual observation of distributions for the first occurrence of ≥50% maturity, and computation of l_t of the von Bertalanffy equation using age at maturity for t. To aid comparisons, we subdivided 32 white sucker (*Catostomus commersoni*) maturity distributions into four types: abrupt transition to maturity (type I), successive increases in proportion mature with increase in age or length (type II), nonsuccessive increases in proportion mature with increase in age or length (type III), and absence of 100% maturity at any age (type IV). Type I distributions were best represented by reporting the first occurrence of ≥50% maturity, types II and III by probit analysis and the maximum likelihood method, and type IV distributions were not adequately represented by any method. Lysack's formula tended to produce high estimates for types II and III and negative values for some type IV distributions. Both the number and position of missing year classes influenced estimates of age at maturity. We recommend documenting maturity distributions with all estimates of age and size at maturity.

Nous avons comparé six méthodes permettant d'évaluer l'âge et la longueur de poissons itéroparеux à maturité sexuelle, soit l'analyse probit, la méthode de la ressemblance maximum, la régression linéaire avec des données transformées (arcsinus–racine carrée), la formule de Lysack, l'observation visuelle des distributions de la première occurrence de 50 % ou plus de maturité, et le calcul de l_t de l'équation de von Bertalanffy utilisant l'âge à maturité comme valeur de t. Pour faciliter les comparaisons, nous avons subdivisé 32 distributions de maturité de meunier noir (*Catostomus commersoni*) en quatre types : transition abrupte à maturité (type I), augmentations successives de la proportion de poissons adultes avec l'augmentation de la longueur ou de l'âge (type II), augmentation non successive de la proportion de poissons adultes avec l'augmentation de l'âge ou de la longueur (type III) et absence de maturité à 100 % à tout âge (type IV). Les distributions de type I étaient mieux représentées en signalant la première occurrence de 50 % ou plus de maturité, celle de type II et III par l'analyse probit et la méthode de la ressemblance maximum, et les distributions de type IV n'étaient pas représentées adéquatement par aucune de ces méthodes. La formule de Lysack tendait à produire des évaluations élevées dans le cas des valeurs négatives de type II et III pour certains types de distribution du type IV. Le nombre et la position des catégories d'années manquantes influencent des évaluations de l'âge à la maturité. Nous recommandons que soit documentée la distribution à maturitée à l'aide de toutes les évaluations d'âge et de taille à maturité.

Received May 31, 1990
Accepted February 20, 1991
(JA589)

Reçu le 31 mai 1990
Accepté le 20 février 1991

Fisheries researchers have long been interested in assigning a single value to represent the age or size at sexual maturity for members of a fish population. Such a value has been customarily obtained from the frequencies of mature fish along a specific segment of a complete age or length distribution. Six methods have been commonly used to generate such estimates of onset of sexual maturity (Lysack 1980; Bowering 1983; Nammack et al. 1985; Goto 1987; Welch and Foucher 1988; Waiwood and Buzeta 1989). However, these methods may be subject to a variety of quantitative factors that have, as yet, not been examined critically. A foremost problem is the possibility that each method may generate a *different* estimate of onset of maturity for the *same* age distribution, with the possibility of one method consistently yielding a higher or lower value.

Differences between ages at sexual maturity that arise due to methodology may seem minor and one might expect that any one of the methods presented is suitable. However, in the context of population production, even small differences of 1 yr or less in age at maturity can be significant in the estimation of future expected yields of commercially exploited fishes (e.g. Welch and Foucher 1988). Moreover, variability in the shape and structure of distributions is likely to occur among populations, with the liability that each method may account for these dissimilarities among distributions in different ways. Thus, the limitations of a method need to be recognized before it is employed to identify the transition from immaturity to maturity. In addition to simply misrepresenting a population's age

[1]Present address: Department of Fisheries and Oceans, Marine Fish Division, Biological Station, St. Andrews, N.B. E0G 2X0, Canada.

TABLE 1. Locations and morhpometric characteristics of the eight study lakes (for additional limnological data, see Trippel and Harvey 1987b, 1989).

Lake	North latitude	West longitude	Maximum depth (m)	Mean depth (m)	Surface area (ha)
Bigwind	45°03′	79°03′	32	10.7	111
Red Chalk	45°11′	78°57′	38	14.2	57
King	45°53′	79°30′	6	2.6	29
George	46°02′	81°24′	37	18.6	148
Chub	45°13′	78°59′	27	8.9	32
Dickie	45°09′	79°05′	12	5.0	92
Crosson	45°05′	79°03′	25	8.4	57
Gullfeather	45°06′	79°01′	13	4.8	66

at maturity, the use of single values and the associated potential risk of error is prevalent in studies concentrating on reproductive strategies and tactics (e.g. Stearns and Crandall 1984), and particularly those reporting connections between age at sexual maturity and other characteristics of the population, species, or environment (Schaffer and Elson 1975; Hutchings and Morris 1985; Roff 1988).

Although our comparative analysis is limited to white sucker (*Catostomus commersoni*), it should help to identify the need to establish consistent methodologies for other iteroparous fishes. This is particularly relevant in comparing life history traits among fish populations that differ in geographical distribution and for detecting changes in closely monitored populations that may be influenced by exploitation or environmental change.

The objectives of this study were to (1) categorize the array of age and length frequency distributions of white sucker, (2) determine which of six methods of estimating age and length at maturity considered in this study were most appropriate for each type of frequency distribution, and (3) establish the effects of variables, such as missing year classes, on these estimates of age and length at sexual maturity.

Methods

White suckers used to construct the age and length frequency distributions were collected April–June 1981–88, from eight south-central Ontario lakes (Table 1). Fish were captured using gill, trammel, fyke, and trap nets. For each fish, sex was determined by gonadal examination, fork length (± 0.1 cm) recorded, and pectoral fin rays removed for age determination (Beamish and Harvey 1969; Chalanchuk 1984). State of gonadal maturation of this spring-spawning species was recorded as immature or mature (Trippel 1984) and mature individuals were either ripe, ripe and running, spent, or had failed to release mature sex products during spawning such that they exhibited gonadal atresia. For adult females of Gullfeather Lake which do not mature every year, those captured in a nonreproductive condition were recorded as immature (Trippel and Harvey 1989). White suckers collected in June that were initiating maturation for the first time in their lives also were categorized as being immature. For each population, both age and fork length frequency distributions were constructed to illustrate state of maturity.

Because of the possibility of sex-specific differences in onset of maturation in the white sucker (Geen et al. 1966; Beamish 1973; Trippel and Harvey 1987a), females and males were treated separately. The distributions presented in this study may be interpreted as being static, i.e. a single collection displaying all sampled cohorts simultaneously, rather than representing the transition from immaturity to maturity of an individual cohort over time, which would have required annual samples from each population over a long time period. Such an extensive sampling program would have perturbed the age class composition of the smaller populations.

We classified the 32 distributions (16 for age and 16 for length) for the purpose of comparing the six methods of estimating onset of sexual maturity. Classifications permitted a more systematic appraisal of methods than if distribution shape and structure were ignored. Distributions were classified into four types. The following description of each type pertains to age frequency distributions, but applies equally to fork length distributions. Type I distributions were characterized by a 66–100% occurrence of maturity among individuals in the youngest age class sampled. A type I distribution, consequently, had an abrupt transition to maturity. For some type I distributions, several of the older age classes showed a lower incidence of maturity than occurred in the youngest age class sampled. Other types (II–IV) of distributions commonly started with zero incidence of maturity at the youngest age sampled. Type II distributions were characterized by successive increases in the proportion of mature fish from 0 to 100% maturity with each increase in age. This kind of distribution typically is reported in textbooks describing general life history parameters of animals. Type III distributions were characterized by nonsuccessive increases in the proportion of mature fish through the transition from 0 to 100% maturity. Consequently, the shape of a type III distribution was characterized by a more uneven transition than evident in type II distributions. Type IV distributions were characterized by a failure to attain 100% maturity at any age class, with many age classes having a proportion of maturity $<50\%$.

Five methods were used to estimate onset of sexual maturation for each of the 16 age distributions and a sixth method was used for length distributions. Probit analysis, which is based on a linear transformation of a sigmoid type curve (Hubert 1984), was used to estimate the age at which 50% of the population matured (Finney 1971, Statistical Package for the Social Sciences (SPSSX), version 3.1). We refer to this method as Probit_{50} which has been used widely in the primary literature, for example for Greenland halibut (*Reinhardtius hippoglossoides*) (Bowering 1983) and haddock (*Melanogrammus aeglefinus*) (Waiwood and Buzeta 1989).

A maximum likelihood method (abbreviated here as MLM_{50}) has been derived recently (Welch and Foucher 1988; Schnute and Richards 1990) to estimate length at 50% maturity for Pacific cod (*Gadus macrocephalus*). We employed their length-based approach to estimate age at 50% maturity by using the sigmoid type model

$$\ln(L) = \sum_{i=1}^{M} (N_i - r_i)\,[\ln(a) - bx_i - \ln(x_i)] - N_i \ln\left(1 + \frac{e^{a-bx_i}}{x_i}\right)$$

where x_i = age (years) of the ith age class in the sample, r_i = number of sexually mature individuals observed in the ith age class, M = total number of age classes, and N_i = total number of individuals sampled in the ith age class. Maximum likeli-

hood parameter estimates of L, a, and b were obtained by minimizing the negative log-likelihood of the above expression. This was done by the simplex search method (Nelder and Mead 1965) using a microcomputer-based Pascal program provided by Dr. David Welch, Pacific Biological Station, Nanaimo, B.C. V9R 5K6. The two sigmoid parameters, a and b, were then used to calculate age at 50% maturity, $X_{0.5}$, by applying the Newton–Raphson iteration to the equation

$$\ln(a) - \ln(X_{0.5}) - b X_{0.5} = 0.$$

The arithmetic slope at the point of 50% maturity, $\phi'(X_{0.5})$, was calculated by

$$\phi'(X_{0.5}) = \frac{b + 1/X_{0.5}}{4}.$$

This is the only method of this study that uses the number of fish sampled from each age class in its computation of age at 50% maturity, thus giving more weight to age classes with large relative to small sample sizes.

Simple linear regression analysis (SAS 1988) was employed to estimate the age at which 50% of fish were mature. Prior to computation, data of each age class were transformed to arcsine(proportion of mature fish)$^{1/2}$ as has been similarly done to estimate length at maturity for spiny dogfish (*Squalus acanthias*) (Nammack et al. 1985). This transformation is used to improve the fit of linear models for this type of data (Sokal and Rohlf 1981). If two contiguous values of 0%, or two contiguous values of 100%, occurred in a distribution, we excluded from the regression analysis the outermost values of 0 and 100%. For example, if a hypothetical distribution comprised the following sets of ages and percentages of mature fish: 1 yr 0%, 2 yr 0%, 3 yr 30%, 4 yr 60%, 5 yr 100%, and 6 yr 100%, then only ages 2–5 were analyzed. However, we included two, nonadjacent age classes of 100% maturity if another age class comprising <100% maturity was situated between them. Regressions were computed as

$$\text{Age (years)} = \beta_0 + \beta_1 \text{ arcsine(proportion of fish mature)}^{1/2}.$$

To estimate age at 50% maturity, 0.50 was inserted into proportion of fish mature. Abbreviated reference to this method is Reg_{50}. The Reg_{50} method was investigated further by regression analysis with additional end points 0 and 100%. This additional analysis, referred to as Reg_{50_2}, was restricted to age distributions.

Lysack's (1980) formula, originally developed for lake whitefish (*Coregonus clupeaformis*), was used to estimate a mean weighted age at onset of sexual maturation (Z_{age}) where

$$Z_{\text{age}} = \frac{A_1K_1 + A_2(K_2 - K_1) + A_3(K_3 - K_2) + \ldots + A_n(K_n - K_{n-1})}{K_1 + (K_2 - K_1) + (K_2 - K_2) + \ldots + (K_n - K_{n-1})}$$

where A_n = age (years) of the nth age class in the sample and K_n = proportion of mature fish in the nth age class. Research on white sucker and lake trout (*Salvelinus namaycush*) has also utilized this formula (Trippel and Harvey 1987a; Fraser and Power 1989).

Finally, we made a visual examination of each distribution in order to record the youngest age at which exactly 50% of the individuals were mature. If no such exact value occurred, the youngest age at which more than 50% were mature was recorded. Abbreviated reference to this method is $\text{Obs}_{\geq 50}$.

Fork length at onset of sexual maturity was estimated for each sex of each white sucker population using six methods. The length frequency distributions utilized comprised 2-cm intervals, e.g. 14.0–15.9 cm. To estimate length at maturity, we simply switched age to length in the formulae Probit_{50}, MLM_{50}, Reg_{50}, Lysack, and $\text{Obs}_{\geq 50}$. A sixth method, also used by Nammack et al. (1985), required two steps. First, the von Bertalanffy growth equation was fitted to age–length data:

$$l_t = L_\infty(1 - e^{-K(t - t_0)})$$

where l_t = length at age t (years), L_∞ = asymptotic length, K = Brody's growth coefficient, and t_0 = age at which theoretical fish length is zero.

Second, the age at onset of sexual maturation (based on the recommended value derived from the appraisal of methods for age distributions) was inserted into the von Bertalanffy equation as the value of t, and the value of l_t, the length at maturity computed.

Values estimated by each of the methods were compared and some of the causes of variation among values for each distribution were identified.

Results

Age at Onset of Sexual Maturation

Extreme variation in age at maturity occurred among the eight white sucker populations (Tables 2 and 3). The sex-specific age frequency distributions of these populations were categorized into four types such that four of these 16 distributions were characterized by an abrupt transition to maturity (type I), six (including Chub Lake females) were of successive increases in the proportion of mature fish with an increase in age (type II), four had nonsuccessive increases in the proportion of mature fish with an increase in age (type III), and two were characterized by nonattainment of 100% maturity at any age (Fig. 1).

Type I: Abrupt transition to maturity. The sigmoidal models Probit_{50} and MLM_{50} failed to represent this type of distribution particularly well. For Bigwind Lake females and males which exhibited a high degree of maturity at all ages (Fig. 1), Probit_{50} generated values that were too low (0.05–0.10 yr) and MLM_{50} did not yield any values (Table 2). Also, for these two distributions, the absence of a significant fit by the Reg_{50} model limited its usefulness (Table 3). For Bigwind Lake suckers, Lysack's method produced estimates that were representative. The Lysack method, however, was inappropriate for Red Chalk Lake suckers which exhibited a precocious segment followed by a slight reduction in the percent mature. $\text{Obs}_{\geq 50}$ produced a value of 1.0 yr for each of the four distributions. This is representative of Bigwind Lake but, in the case of Red Chalk Lake, $\text{Obs}_{\geq 50}$ did not represent the decline in maturity at some of the older ages. Consequently, type I distributions having a polymodal structure are not simple to represent by any method.

Type II: Successive increases in the proportion of mature fish with increase in age. For each type II distribution, the five estimates were generally not as widespread as they were for each type I distribution (Fig. 2). Probit_{50} and MLM_{50} generated values that were nearly equivalent (0.04–0.14 yr apart) (Table 2). Reg_{50} values nearly equalled (≤0.08 yr) or were higher (up to 0.52 yr) than values obtained by the sigmoid curve models. Lysack's method generated the highest estimates for four of the six age distributions (Fig. 2). The age distribution

TABLE 2. Results of probit analysis ($Probit_{50}$) and the maximum likelihood method (MLM_{50}) used to estimate age at 50% maturity for four types of white sucker maturity distributions. The definitions of these four types of distributions are provided in the Methods section. a and b are the maximum likelihood estimates of the sigmoid parameters, $X_{0.5}$ and $\phi'(X_{0.5})$ are the derived statistics median length at maturity and slope, $-\ln(L)$ is the value of the likelihood function at the maximum, and n is the sample size. NA = no estimate attained.

Lake	Sex	Age at 50% maturity		Sigmoid parameters of MLM_{50}				
		$Probit_{50}$ (yr)	MLM_{50} (yr)	a	b	$-\ln(L)$	$\phi'(X_{0.5})$	n
Abrupt transition to maturity (type I)								
Bigwind	Female	0.10	NA	3.30×10^{0}	0.009	40.2	NA	154
	Male	0.05	NA	2.10×10^{0}	−0.015	22.4	NA	67
Red Chalk	Female	2.17	3.13	4.75×10^{2}	0.087	20.1	0.102	79
	Male	1.28	2.20	1.36×10^{2}	0.083	8.7	0.134	43
Successive increases in proportion of mature fish with increase in age (type II)								
King	Female	3.55	3.64	7.80×10^{6}	0.337	14.8	0.153	278
	Male	2.30	2.34	1.53×10^{4}	0.277	7.2	0.191	60
George	Female	3.71	3.80	2.70×10^{4}	0.173	39.1	0.109	88
Chub	Female	3.20	3.25	3.01×10^{3}	0.140	31.6	0.077	68
	Male	2.19	2.18	1.78×10^{2}	0.096	27.5	0.139	35
Dickie	Female	6.76	6.90	2.48×10^{3}	0.052	16.2	0.049	38
Nonsuccessive increases in proportion of mature fish with increase in age (type III)								
Crosson	Female	3.26	3.28	8.68×10^{2}	0.100	28.9	0.101	48
	Male	2.53	2.53	7.17×10^{2}	0.132	13.6	0.132	44
George	Male	2.77	2.89	7.61×10^{2}	0.113	36.3	0.115	67
Dickie	Male	6.40	6.50	6.68×10^{4}	0.107	21.7	0.065	52
Nonattainment of 100% maturity at any age (type IV)								
Gullfeather	Female	0.79	NA	3.00×10^{1}	−0.032	47.1	NA	114
	Male	11.15	7.51	5.66×10^{2}	0.027	28.6	0.040	56

of King Lake females was used to depict the unrepresentative older age at maturity that resulted from the use of Lysack's method. Specifically, Lysack's value was 4.19 yr, yet mature fish comprised 14% at 3 yr, 67% at 4 yr, and 100% at 5 yr. The $Probit_{50}$ estimate was 3.55 yr, 0.64 yr younger than Lysack's estimate. $Obs_{\geq 50}$ values were highly variable relative to the other estimates and of little use as a single estimate of maturity (Fig. 2). The recommended methods were $Probit_{50}$ and MLM_{50}.

Type III: Nonsuccessive increases in the proportion of mature fish with an increase in age. Estimates for specific distributions differed by as little as 0.81 yr for Crosson Lake females and by up to 1.08 yr for Crosson Lake males (Tables 2 and 3; Fig. 2). $Probit_{50}$ and MLM_{50} yielded similar estimates and tended to be among the lowest. For type III distributions, the Reg_{50} method rarely resulted in as close a fit in terms of r^2 as when this method was applied to type II distributions. Nevertheless, the Reg_{50} method provided statistically significant equations ($P < 0.05$) for type III distributions. Lysack's values generally were high, although not always misrepresentative. Because type III distributions were in some instances highly irregular, it is difficult to recommend any one method that is suitable for these distributions. This is exemplified using the age distributions of Crosson Lake females: 30% mature at age 3 yr and 90% at age 4 yr, yet at age 5 yr, there occurred a decrease in the proportion of mature fish to 67% and then up to 100% at ≥6 yr. Values obtained were as follows: 3.26 yr by $Probit_{50}$, 3.78 yr by MLM_{50}, 3.63 yr by Reg_{50}, 4.07 yr by Lysack's formula, and 4.0 yr by $Obs_{\geq 50}$.

Type IV: Nonattainment of 100% incidence of maturity at any age. This type of maturity distribution occurred for both sexes of the Gullfeather Lake population (Fig. 1). The highest age-specific level of maturity was 46% at age 5 yr for females and 60% at age 8 yr for males. None of the methods yielded useful estimates. $Probit_{50}$ values were too low or too high. A MLM_{50} value was unobtainable for one of the two distributions. Reg_{50} estimates seemed appropriate but the r^2 values were only 0.00 and 0.01 and Lysack's values were negative or far too low, with one being negative. For females, no value of $Obs_{\geq 50}$ was obtainable. We recommend that only raw data be presented for distributions such as these.

Length at Onset of Sexual Maturation

Estimates from six methods varied considerably for specific distributions (Fig. 3), ranging from 19.0–26.0 cm for Red Chalk Lake females to 14.6–29.5 cm for Bigwind Lake males (Tables 4 and 5; Fig. 4).

Type I: Abrupt transition to maturity. Neither the $Probit_{50}$ nor MLM_{50} method accounted for the sudden onset of maturity evident in type I distributions. Reg_{50} estimates were all derived from nonsignificant equations ($P >> 0.05$) and were high. Lysack's method represented the precocity of Bigwind Lake suckers but it generated high values for distributions which had intermediate size classes of decreased frequency of maturity.

TABLE 3. Results of three methods used to estimate ages at onset of sexual maturation for four types of white sucker maturity distributions. The definitions of these four types of distributions are provided in the Methods section. The three methods employed were (1) simple linear regression analysis on transformed data of the proportion of mature fish in each age class (age (yr) = β_1 arcsine(proportion of fish mature)$^{1/2}$ + β_0; estimates were calculated for ages when 0.50 of fishes were mature (Reg_{50}); the lower equation for each distribution was calculated, where possible, using data on two additional age classes, i.e. an extra 0 and 100% at each end of the distribution (Reg_{50_2}); for many distributions, however, only one additional age class could be included at either the young or the old end of the distribution; (2) Lysack's formula (see Methods section for details); and (3) occurrence of the youngest age at which >50% of fishes were mature by direct observation of the distributions in Fig. 1 ($Obs_{\geq 50}$) (underscored values represent the youngest ages at which exactly 50% were mature). SE = standard error; n = number of age classes used in the Reg_{50} and Reg_{50_2} methods; $^*P < 0.05$; $^{**}P < 0.01$; NS = not significant.

Lake	Sex	Reg_{50} and Reg_{50_2} (yr)	Parameter estimates of Reg_{50} and Reg_{50_2} β_1 (mean (SE))	β_0 (mean (SE))	n	r^2	Lysack (yr)	$Obs_{\geq 50}$ (yr)
			Abrupt transition to maturity (type I)					
Bigwind	Female	−0.73	0.13 (0.09)	−6.58 (6.78)	5	0.40 NS	1.36	1.0
		1.69	0.05 (0.02)	−0.56 (1.50)	6	0.57 NS		
	Male	2.94	−0.013 (0.070)	3.53 (5.62)	4	0.02 NS	1.26	1.0
		2.47	0.016 (0.053)	1.75 (4.19)	5	0.02 NS		
Red Chalk	Female	2.69	0.037 (0.036)	1.02 (2.06)	5	0.26 NS	3.12	1.0
		2.73	0.054 (0.027)	0.30 (1.73)	6	0.49 NS		
	Male	2.12	0.042 (0.030)	0.24 (2.06)	5	0.40 NS	2.25	1.0
		2.06	0.056 (0.028)	−0.46 (2.07)	6	0.50 NS		
			Successive increases in proportion of mature fish with increase in age (type II)					
King	Female	3.63	0.033 (0.02)	2.14 (0.13)	4	0.99**	4.19	4.0
		3.65	0.042 (0.07)	1.76 (0.37)	6	0.91**		
	Male	2.38	0.035 (0.03)	0.808 (0.213)	4	0.99**	2.88	3.0
		2.58	0.039 (0.06)	0.824 (0.424)	5	0.92**		
George	Female	3.65	0.033 (0.06)	2.16 (0.30)	4	0.94*	4.35	5.0
		3.64	0.044 (0.06)	1.66 (0.36)	6	0.92**		
Chub	Female	3.57	0.063 (0.09)	0.73 (0.45)	5	0.95**	4.07	4.0
	Male	2.40	0.034 (0.05)	0.87 (0.29)	4	0.96*	2.78	2.0
Dickie	Female	7.28	0.06 (0.01)	4.58 (0.74)	6	0.83*	8.02	6.0
		7.36	0.07 (0.01)	4.21 (0.51)	8	0.90**		
			Nonsuccessive increases in proportion of mature fish with increase in age (type III)					
Crosson	Female	3.74	0.041 (0.01)	1.89 (0.04)	5	0.82*	4.07	4.0
		3.66	0.05 (0.01)	1.41 (0.52)	7	0.88*		
	Male	3.44	0.035 (0.014)	1.85 (0.94)	5	0.69 NS	3.46	4.0
		3.70	0.047 (0.020)	1.58 (1.43)	6	0.60 NS		
George	Male	2.92	0.042 (0.06)	1.03 (0.36)	5	0.94**	3.46	4.0
		2.95	0.053 (0.07)	0.56 (0.38)	6	0.93**		
Dickie	Male	6.13	0.045 (0.010)	4.11 (0.52)	5	0.87**	6.72	7.0
		6.10	0.055 (0.08)	3.62 (0.42)	7	0.92**		
			Nonattainment of 100% maturity at any age (type IV)					
Gullfeather	Female	6.37	−0.028 (0.085)	7.63 (2.16)	11	0.01 NS	−3.74	—[a]
		5.52	−0.080 (0.078)	9.12 (1.90)	12	0.09 NS		
	Male	7.67	0.002 (0.067)	7.66 (2.11)	9	0.0 NS	3.60	8.0
		7.84	0.033 (0.065)	6.35 (1.93)	10	0.03 NS		

[a]Does not attain 50% sexually mature at any age class.

$Obs_{\geq 50}$ provided a suitable estimate for some type I distributions although it was not representative when incidence of maturity decreased at intermediate sizes. The von Bertalanffy method, which uses age at maturity for t in the equations of Table 6, represented the decrease in maturity at intermediate sizes but it did not generate small lengths characteristic of precocity. We suggest that Lysack's method and $Obs_{\geq 50}$ are useful for type I distributions that maintain a high level of maturity at larger sizes. No method is recommended for type I distributions that have an intermediate zone of lower maturity.

Type II: Successive increases in the proportion of mature fish with increase in length. The six estimates of length at maturity for specific type II distributions were generally not so widespread as the estimates derived for specific type I and III distributions (Fig. 4). Using the six methods for the six type II length distributions, the largest spread among estimates was for King Lake males: 22.5–27.0 cm, a 4.5-cm difference. $Probit_{50}$ and MLM_{50} yielded very similar estimates: only 0.0–0.3 cm apart for any one distribution. These two sigmoid curve based methods yielded the lowest values for King Lake females and

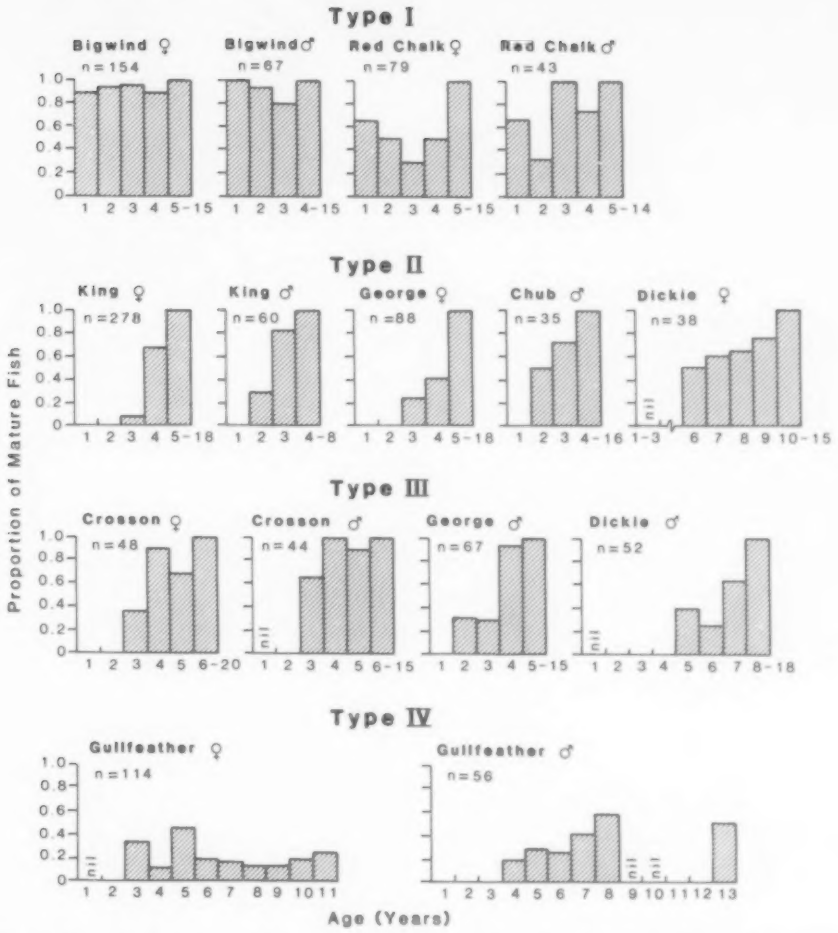


FIG. 1. Proportion of mature fish in each age class of female and male white suckers collected from eight lakes. The maturity distributions were categorized into four types: abrupt transition to maturity (type I), successive increases in proportion of mature fish with increase in age (type II), nonsuccessive increases in proportion of mature fish with increase in age (type III), and nonattainment of 100% maturity at any age (type IV). n = sample size; nil = no fish sampled of this age class. A more detailed definition of distribution type is given in the Methods section.

Dickie Lake males in which a change from 0 to 60% maturity occurred between adjacent length intervals. Other methods did not adequately account for this change and hence were considered inferior to the sigmoid models. Lysack's formula generated relatively high values. Estimates made by the von Bertalanffy based method (Table 5) were inconsistent in their magnitude when related to estimates of sigmoid curve models (Table 4).

Type III: Nonsuccessive increases in the proportion of mature fish with increase in length. Fifty percent of all length distributions were of type III. Estimates of length at maturity for specific distributions differed substantially for six of the eight distributions; for example, values ranged from 23.0 to 35.9 cm for George Lake males. There was a greater spread among values of type III length distributions than type III age distributions. This is because, relative to age distributions, there was a greater incidence of missing length intervals (no fish captured) and there occured a higher degree of irregularity in the maturation pattern of length distributions, such as sudden shifts down to 0% maturity (Fig. 1 and 3). Consequently, an estimate of length at 50% maturity, derived by many methods, was poorly suited to represent some of the type III length distributions (e.g. Chub Lake females, Crosson Lake females and males, Dickie Lake females, and Gullfeather Lake males). Sigmoid curve based estimates typically generated the most sensible estimates of length at 50% maturity. For Reg_{50}, the r^2 values for type III distributions were lower than those of type II estimates. $Obs_{\geq 50}$ values were inconsistent, i.e. appropriate for some distributions (e.g. Dickie Lake females), yet inappropriate for others (e.g. George Lake males).

Additional Factors for Consideration in Estimation of Onset of Sexual Maturation

Regression analysis with additional end points is a potential cause of variability among estimates of age at maturity. Occasionally, researchers have used broader ranges of age classes to obtain estimates of onset of sexual maturity. There are no

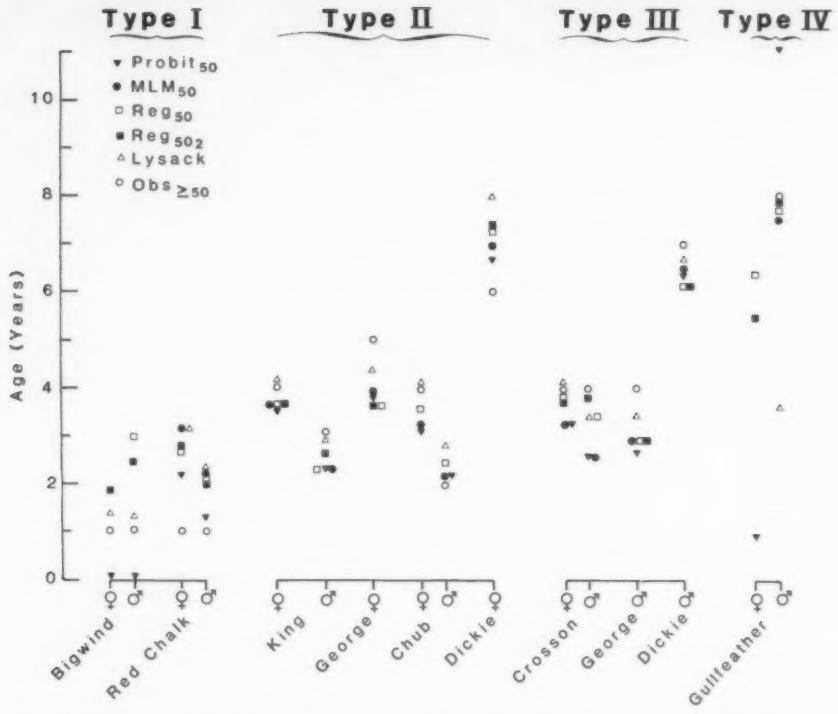


FIG. 2. Comparison of estimates of age at maturity derived by a variety of methods for the maturity distributions of Fig. 1. The methods used were (1) probit analysis ($Probit_{50}$) (Finney 1971), (2) maximum likelihood method (MLM_{50}) (Welch and Foucher 1988), (3) linear regression analysis on arcsine-square root transformed data with one end point at each of 0 and 100% maturity (Reg_{50}) (Nammack et al. 1985) and with more than one end point at 0 and 100% maturity (Reg_{50_2}), (4) Lysack's (1980) formula for mean weighted age at maturity, and (5) visual observation of the distribution for the first occurrence of ≥50% maturity ($Obs_{\geq 50}$). Negative values of age maturity (see Table 3) were not presented.

strict rules as to where to commence and cease using data from a frequency distribution for this purpose. Lysack's formula makes no use of additional young or old age classes if there is no change in the proportion of fish mature in adjacent age classes, e.g. $8(1.00 - 0.90) + 9(1.00 - 1.00)$ becomes $0.80 + 0$. However, the inclusion of additional end points in the Reg_{50} method may result in different estimates of age at maturity. For each of the 16 age distributions, Reg_{50} was recomputed with additional young and/or old age classes. For some distributions, two additional values were included, one at each of the extreme ends of the distribution, and resulting equations are referred to as Reg_{50_2}. For type I distributions, this procedure did not result in significant equations ($P > 0.05$; Table 3. Moreover, for type II–IV distributions, a comparison of r^2 values derived from the Reg_{50} and Reg_{50_2} methods revealed only minor differences (Table 3).

Generation of atypically low or negative values by Lysack's method is a concern (Table 3). In distributions that are characterized as type IV, i.e. nonattainment of 100% maturity, the Lysack value of age at maturity tends to be exceedingly low, as a consequence of the influence exerted by the last computed $A_1(K_1 - K_2)$. To demonstrate this, the two Gullfeather Lake age distributions were reanalyzed after altering their final ages to a 100% incidence of maturity. For the female distribution, this meant adjusting the proportion of mature fish at age 12 yr from 0 to 1.00. This resulted in the Lysack age estimate increasing from −3.74 to 5.26 yr. The additional 9 yr was a result of the final computation of $12(1.00 - 0.25)$. For males, the proportion of mature fish at age 13 yr was elevated from 0.50 to 1.00. This resulted in the Lysack estimate increasing from 3.60 to 10.10 yr, the additional 6.5 yr resulting from $13(0.50 - 0.00)$.

Missing year classes is a phenomenon not uncommon among fish populations. Of particular relevance to estimates of maturity are the year classes falling within the progression from immaturity to maturity. If one or more of these is missing, estimates of age at maturity may be affected. An example of a distribution with missing year classes was Chub Lake females (Fig. 5), where 13% of fish were mature at age 2, 34% at age 3, 82% at age 4, but no fish of ages 5 and 6 were captured, and 100% were mature for ages 7–19 yr. The $Probit_{50}$ value for this distribution was 3.2 yr, the MLM_{50} was 3.25 yr, for Reg_{50} it was 3.57 yr, and for Lysack's it was 4.07 yr. We manipulated these data to determine whether ages at maturity would change if one of the two missing year classes (age 6 yr) was substituted with 100% maturity. The result was a decrease in age at maturity: $Probit_{50}$ from 3.20 to 3.13 yr (down 2.2%), MLM_{50} from 3.25 to 3.23 yr (down 0.6%), Reg_{50} from 3.57 to 3.34 yr (down 6.5%), and Lysack's from 4.07 to 3.89 yr (down 4.4%). By substituting 100% maturity at both ages 5 and 6 yr, age at maturity decreased further: $Probit_{50}$ from 3.20

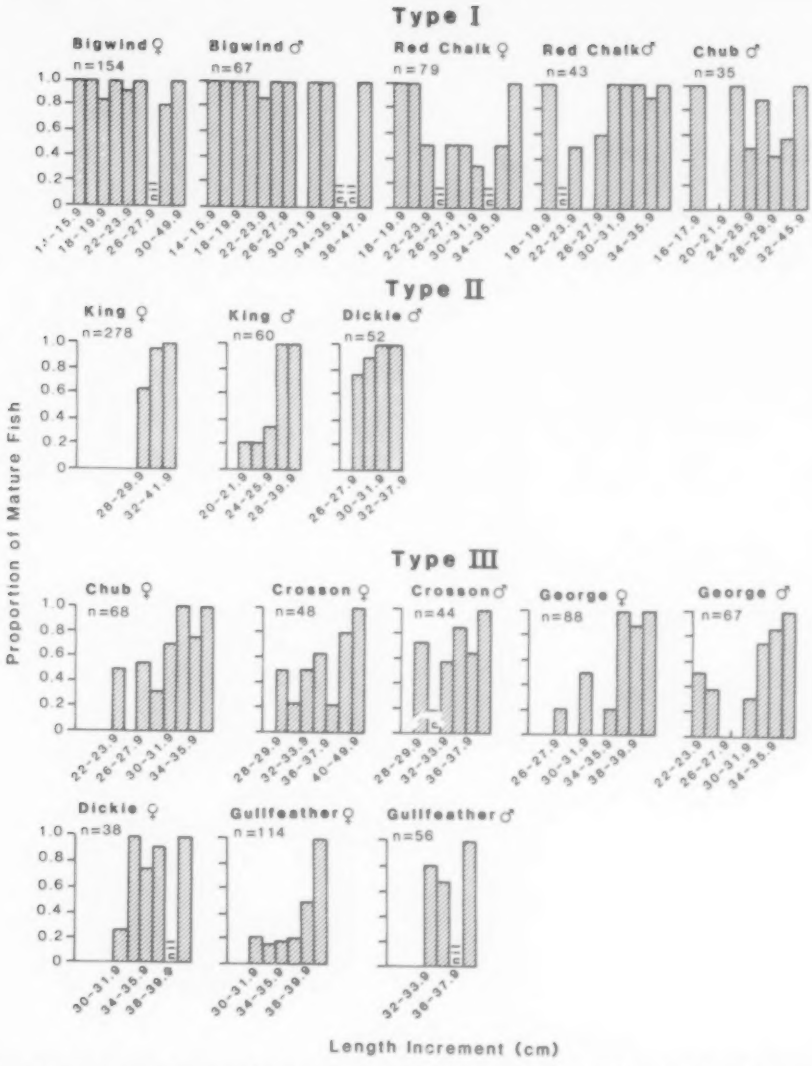


FIG. 3. Proportion of mature fish in each fork length increment of female and male white suckers collected from eight lakes. The maturity distributions were categorized into three types: abrupt transition to maturity (type I), successive increases in proportion of mature fish with increase in length (type II), and nonsuccessive increases in proportion of mature fish with increase in length (type III). n = sample size; nil = no fish sampled of this length increment. A more detailed definition of distribution type is given in the methods section.

to 3.08 yr (down 3.8%), MLM_{50} from 3.25 to 3.19 yr (down 1.8%), Reg_{50} from 3.57 to 3.11 yr (down 12.8%), and Lysack's from 4.07 to 3.71 yr (down 8.8%). Of the four methods, the sigmoid curve based methods were the least sensitive to the presence of missing year classes. In Reg_{50}, the higher maturity values resulted from missing values for specific ages in the regression analysis. With year classes missing, the outermost point in the regression was at a greater distance from the origin of the two axes, reducing the slope of the fitted line, and making higher the estimated age at 50% maturity. For Lysack's method, the higher values resulting from missing year classes are a result of the $A_1(K_1 - K_2)$ portion of the formula. With two consecutive missing year classes, the last value of A_1 used to multiply $(K_1 - K_2)$ is 2 yr higher than occurs if no year class is missing. The absence of year classes in Chub Lake has been observed before. For example, a sample of 58 suckers in 1979 included no 4-yr-old fish.

The position of a missing year class may be important through its effect on estimations of age at onset of maturity. Again, this can be illustrated using the age distribution of Chub Lake females. We shifted the missing year class from age 5 yr to age 4 yr and replaced the second missing year class with a 100% incidence of maturity. The resulting proportions of fish mature in each of the age classes were thus age 1 yr 0%, 2 yr 13%, 3 yr 34%, 4 yr nil, 5 yr 82%, and 6 yr 100%. This shifting in the missing year class to 1 yr earlier resulted in a shift to older

TABLE 4. Results of probit analysis ($Probit_{50}$) and the maximum likelihood method (MLM_{50}) used to estimate fork length (FL) at 50% maturity for three types of white sucker maturity distributions. The definition of each type of maturity distribution is provided in the Methods section. a and b are the maximum likelihood estimates of the sigmoid parameters, $X_{0.5}$ and $\phi'(X_{0.5})$ are the derived statistics median length at maturity and slope, $-\ln(L)$ is the value of the likelihood function at the maximum, and n is the sample size. NA = no estimate attained.

Lake	Sex	Length at 50% maturity		Sigmoid parameters of MLM_{50}				
		$Probit_{50}$ (FL, cm)	MLM_{50} (FL, cm)	a	b	$-\ln(L)$	Slope $\phi'(X_{0.5})$	n
Abrupt transition to maturity (type I)								
Bigwind	Female	18.6	NA	9.21×10^{-1}	−0.039	23.1	NA	154
	Male	NA	NA	9.51×10^{-1}	0.032	5.1	NA	67
Red Chalk	Female	24.0	NA	4.83×10^{0}	−0.053	14.3	NA	79
	Male	21.1	19.5	2.09×10^{2}	0.121	12.3	0.043	43
Chub	Male	23.5	25.1	3.19×10^{3}	0.193	27.2	0.058	35
Successive increases in proportion of mature fish with increase in age (type II)								
King	Female	28.4	28.7	1.74×10^{20}	1.506	9.7	0.385	278
	Male	24.3	24.5	5.40×10^{8}	0.691	8.3	0.183	60
Dickie	Male	26.5	26.5	1.34×10^{13}	1.02	6.0	0.264	52
Nonsuccessive increases in proportion of mature fish with increase in age (type III)								
Chub	Female	28.5	28.2	4.92×10^{4}	0.265	18.0	0.075	68
Crosson	Female	33.5	33.8	9.11×10^{4}	0.234	17.6	0.066	48
	Male	NA	27.1	1.57×10^{3}	0.150	14.6	0.047	44
George	Female	36.6	33.8	3.65×10^{6}	0.343	29.8	0.093	88
	Male	29.7	30.8	2.56×10^{6}	0.368	24.8	0.100	67
Dickie	Female	32.5	32.5	4.59×10^{9}	0.577	18.1	0.152	38
Gullfeather	Female	39.1	38.8	2.17×10^{6}	0.282	48.3	0.077	114
	Male	26.5	31.4	4.96×10^{7}	0.454	18.1	0.121	56

ages at maturity: $Probit_{50}$ from 3.20 to 3.52 yr (up 9.1%), MLM_{50} from 3.25 to 3.45 yr (up 6.2%), Reg_{50} from 3.34 to 3.55 yr (up 6.3%), and Lysack's from 3.89 to 4.37 yr (up 12.3%).

Discussion

If shifts in onset of maturity of fishes are to be examined in relation to latitude (Leggett and Carscadden 1978), length of migration (Roff 1988), exploitation (Nikol'skii 1962; Spangler et al. 1977; Diana 1983), heavy metal contamination (McFarlane and Franzin 1978; Munkittrick and Dixon 1989), lake acidity (Trippel and Harvey 1987a), as well as other factors, then a common strategy should be established to assess onset of sexual maturation. The methods currently used to determine onset of maturity in the primary literature should not be employed indiscriminantly to frequencies of mature fish across age classes, but rather the choice of method should be based in part on the structure of the distribution. This study yielded four distinct types of maturity distributions for white sucker, ranging from abrupt transition to nonattainment of 100% maturity at any age. The method or methods recommended for each type of distribution are identified in Table 7.

Each type of distribution may have arisen from a number of circumstances. Type I distributions often are characteristics of fish populations with precocious fish, although they may also be representative of populations that are characterized by both a precocious segment and a relatively late-maturing segment. A sudden increase in the food supply for juvenile white suckers may permit early maturity and thus development from one of the other types of distributions toward a type I distribution. There is also the potential that if the first age class in a type I distribution is not very young, the technique employed to sample small fish was inadequate. Type II distributions generally represent populations that are in a stable condition in which the proportions of mature fish reflect those which would occur from a time series of a single year class in which a gain in percent maturity occurs with each passing year. The complexity and, at times polymodal structure, of type III distributions suggests that single values are of limited use in representing some of the type III maturity distributions. Maturing at relatively younger ages by individuals of some year classes, as opposed to later maturity among individuals of other year classes, is a probable source of type III distributions. Poor sampling of certain age (or length) classes may also be a contributing factor in type III distributions. Furthermore, the variable proportion of mature fish among adjacent age classes may be a result of variable growth rates of individuals of different cohorts. Type IV distributions are characteristic of populations that have slow-growing individuals. Many of the white suckers of the high-density Gullfeather Lake population were in an impoverished condition such that they gained an insufficient amount of energy from their depauperate food supply to permit gonadal maturation (Trippel and Harvey 1989).

Some consideration must also be made of the usefulness of a single value in representing onset of maturity. Several type I and all of type IV distributions were generally very difficult to represent by a single value, and we also experienced difficulty

TABLE 5. Results of four methods used to estimate fork length (FL) at onset of sexual maturation for three types of white sucker maturity distributions. The definitions of these three types of distributions are provided in the Methods section. The four methods employed were (1) simple linear regression analysis on transformed data of the proportion of mature fish in each fork length interval (fork length (cm) = β_1 arcsine(proportion of fish mature)$^{1/2}$ + β_0); estimates were calculated for ages when 0.50 of fishes were mature (Reg_{50})); (2) Lysack's formula (see Methods section for details); (3) occurrence of the smallest fork length interval at which ≥50% of fishes were mature by direct observation of the distributions in Fig. 3 ($Obs_{\geq 50}$) (underscored values represent the smallest fork length interval at which exactly 50% were mature); and (4) the parameter l_t of the von Bertalanffy growth equation was estimated using age at maturity as t. SE = standard error; n = number of age classes used for the Reg_{50} method; *$P < 0.05$; **$P < 0.01$; NS = not significant.

Lake	Sex	Reg_{50} (FL, cm)	Parameter estimates of Reg_{50} β_1 (mean (SE))	β_0 (mean (SE))	n	r^2	Lysack (FL, cm)	$Obs_{\geq 50}$ (FL, cm)	l_t of von Bertalanffy (FL, cm)
Abrupt transition to maturity (type I)									
Bigwind	Female	26.5	−0.10 (0.19)	30.97 (16.07)	8	0.05 NS	16.5	15.0	15.2
	Male	29.5	−0.10 (0.09)	34.00 (7.50)	11	0.13 NS	14.6	15.0	15.6
Red Chalk	Female	27.2	−0.10 (0.07)	27.4 (4.3)	10	0.00 NS	26.7	19.0	25.9
	Male	26.0	0.11 (0.05)	21.03 (3.69)	10	0.34 NS	22.4	19.0	21.5
Chub	Male	23.8	0.07 (0.05)	20.64 (3.04)	10	0.19 NS	23.4	17.0	30.1
Successive increases in proportion of mature fish with increase in length (type II)									
King	Female	29.9	0.08 (0.02)	26.32 (1.47)	5	0.82*	29.9	29.0	29.5
	Male	23.9	0.09 (0.02)	19.92 (1.12)	5	0.81*	25.4	27.0	22.5
Dickie	Male	27.3	0.06 (0.02)	24.57 (1.09)	4	0.87 NS	27.7	27.0	28.6
Nonsuccessive increases in proportion of mature fish with increase in length (type III)									
Chub	Female	28.7	0.14 (0.04)	22.42 (2.00)	9	0.69**	28.6	23.0	32.8
Crosson	Female	33.9	0.16 (0.04)	22.6 (2.1)	8	0.72**	34.5	29.0	36.2
	Male	32.2	0.12 (0.05)	26.8 (2.9)	6	0.62 NS	31.5	29.0	34.0
George	Female	33.8	0.12 (0.03)	28.4 (1.7)	9	0.64*	34.8	31.0	32.6
	Male	29.0	0.16 (0.07)	21.8 (3.2)	9	0.46*	30.9	23.0	35.9
Dickie	Female	33.3	0.10 (0.04)	28.8 (2.4)	6	0.63 NS	31.7	33.0	32.2
Gullfeather	Female	30.4	0.13 (0.04)	30.52 (1.60)	7	0.72*	38.4	339.0	—[a]
	Male	32.6	0.10 (0.03)	28.1 (1.6)	6	0.73*	34.0	33.0	—[a]

[a]A suitable value for t from Tables 2 and 3 was unavailable.

in fully representing the maturity patterns of some type II and III distributions by single values. This problem is clearly shown by the examples of *different* distributions having the *same* or very similar ages at maturity through use of the same method (Table 8). We therefore suggest that it is insufficient simply to present an estimate of onset of maturity without concurrently presenting the proportion of mature fish in each age class.

There is perhaps a need to develop an alternative method of representing onset of maturity for white sucker populations, given the frequency of maturation distributions with irregular structure (i.e. other than type II) and the difficulty in representing their maturity schedule by a single value. Worth consideration is a study framework based on individuals. Future research on maturation of white suckers could be directed towards understanding why an individual matured as opposed to deriving a collective, single estimate of maturity for a population. For example, a study on Gullfeather Lake suckers using the procedure of backcalculation on cross-sections of pectoral fin rays to reconstruct an individual's growth history holds promise of uncovering causes of maturity (Trippel and Harvey 1989). Specifically, we found a significantly greater annual soma mass increment in population members exhibiting maturity relative to those which failed to do so, and the magnitude of this increment was a negative function of absolute soma mass. Exploration of approaches that jointly combine age and length at maturity may also lead to significant advancements over using single values of age and length at maturity (Stearns and Koella 1986; Richard et al. 1990).

In earlier work on lakes with maximum depths in excess of 24 m (Trippel and Harvey 1987a), we outlined the biological interpretation of the maturity patterns in five white sucker populations. White suckers in three acidified lakes (George, Crosson, and Chub) frequently matured at older ages and larger body sizes than white suckers in two circumneutral lakes (Bigwind and Red Chalk). In the acid lakes, adults experienced high postspawning mortality, even though they were of moderate age and large body size. Large body size of spawners in acid lakes was linked to a combination of low white sucker density and an abundance of suitable chironomid prey (Logan et al. 1991) which permitted rapid somatic growth (Trippel and Harvey 1987b). We speculated that the late maturity observed in acid lake populations was a life history strategy that made possible a single, relatively large reproductive effort prior to high postspawning mortality.

Time of year during which white suckers were sampled is critical to making estimates of onset of maturity. In south-central Ontario, white suckers typically spawn during the first 2 wk of May. If a sucker's maturity state in May is known,

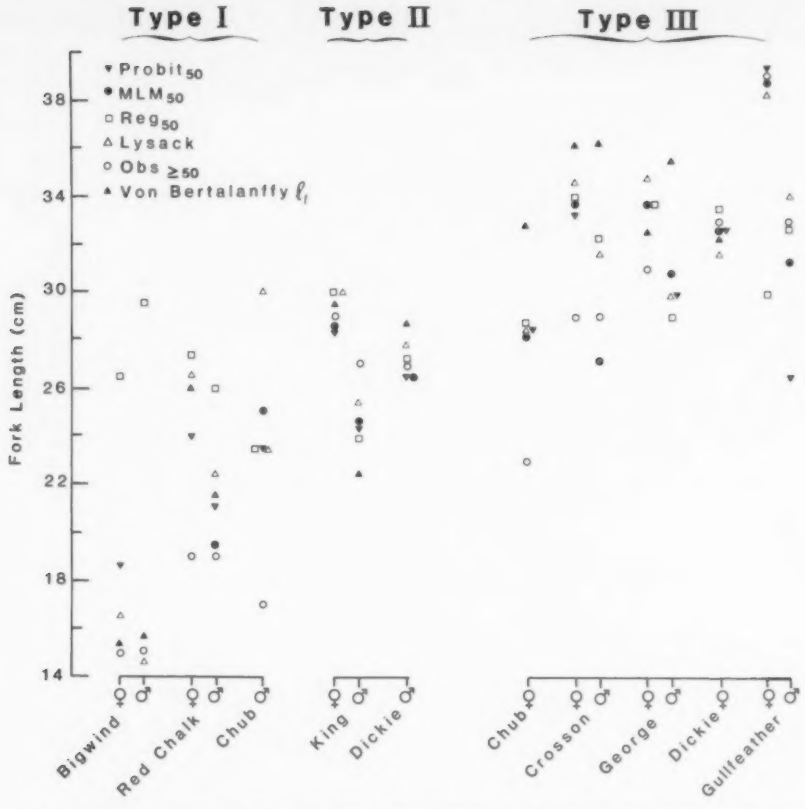


FIG. 4. Comparison of estimates of length at maturity derived by a variety of methods for the maturity distributions of Fig. 3. The methods used were (1) probit analysis ($Probit_{50}$) (Finney 1971), (2) maximum likelihood method (MLM_{50}) (Welch and Foucher 1988), (3) linear regression analysis on arcsine-square root transformed data with one end point at each of 0 and 100% maturity (Reg_{50}) (Nammack et al. 1985), (4) Lysack's (1980) formula for mean weighted age at maturity, (5) visual observation of the distribution for the first occurrence of ≥50% maturity ($Obs_{\geq 50}$), and (6) the parameter l_t of the von Bertalanffy equation estimated using age at maturity for t (Nammack et al. 1985).

then the data on this individual can be used in estimates of age and length at maturity. Adults collected in June still appear spawned out, thus permitting indirect determination of the May maturity state. When an individual is collected in July, however, gametogenesis in adults is sufficiently advanced that it is no longer possible to determine if each individual had spawned earlier in the year. If an individual collected later than June is to be included in calculations, then 1 yr should be added to its age; however, by doing this, one assumes that this individual would have survived until May of the following year — a serious shortcoming in the use of summer-collected specimens. Also, estimates of length at maturity would be biased positively by using July-collected fish. Therefore, restricting fish collections to the period from mid-April (approximately ice-out in the study area) to late June was ideal. This coincided also with annulus formation on the pectoral fin rays.

The methods employed in this study rely on accurate estimates of the proportion of mature fish in each age class and require a large sample of each age class, especially of age classes that comprise both immature and mature individuals. Unfortunately, this is not always possible because of weak or missing year classes or sampling biases due to fishing gear. The liabilities of poor sampling have been discussed by Welch and Foucher (1988). For an extreme case where the actual proportion mature of a certain age class in the population equals 0.10 and only two fish for this age class have been sampled, there are only three possible proportions that can be obtained from the data: 0, 0.50, and 1.00, none of which matches 0.10. The larger the sample size, the greater the chance that the sample will approach the actual proportion of mature fish in the population. It is noteworthy that extensive sampling of large marine fish populations permits subdivisons of the catch into length intervals as small as 0.5 cm (e.g. Schnute and Richards 1990). This is in contrast with small populations (500–2000 fish) which often are the focus of study of maturation changes; yet, within these small, and at times stressed, populations, few fish are available for sampling to determine sex and state of maturity (Trippel and Harvey 1987a, 1987b, 1990; Munkittrick and Dixon 1989).

Testing for a significant difference between two values of onset of maturity is an important issue. For frequency distributions (type II in particular) for which $Probit_{50}$ suitably represented onset of maturity, we recommend using the relative median potency analysis (Finney 1971, SPSSX, version 3.1) for determining whether onset of sexual maturity differs between two populations. We also recommend use of the

TABLE 6. Parameter estimates (mean ± 1 SE) of the von Bertalanffy growth equation for female and male white suckers of eight lakes. L_∞ = asymptotic length, K = Brody's growth coefficient, t_0 = age at which theoretical fish length is zero, and n = number of fish used in determinations. All equations have $r^2 > 0.95$ and are significant at $P < 0.0001$.

Lake	L_∞ (FL, cm)	K	t_0 (yr)	n
		Female		
Bigwind	47.6 ± 1.4	0.231 ± 0.035	−0.291 ± 0.427	154
Red Chalk	45.5 ± 1.1	0.318 ± 0.047	0.476 ± 0.301	79
King	38.7 ± 0.7	0.414 ± 0.086	0.613 ± 0.511	278
George	52.7 ± 2.7	0.159 ± 0.318	−2.401 ± 0.675	88
Chub	44.1 ± 0.8	0.424 ± 0.059	0.361 ± 0.284	68
Dickie	36.1 ± 0.6	0.244 ± 0.045	−1.875 ± 0.835	38
Crosson	48.9 ± 2.0	0.240 ± 0.069	−2.007 ± 1.159	48
Gullfeather	35.6 ± 0.7	0.363 ± 0.045	0.464 ± 0.243	114
		Male		
Bigwind	45.3 ± 1.9	0.251 ± 0.055	−0.421 ± 0.515	67
Red Chalk	41.7 ± 0.6	0.409 ± 0.053	0.481 ± 0.276	43
King	36.0 ± 0.9	0.373 ± 0.084	−0.253 ± 0.602	60
George	44.6 ± 1.2	0.408 ± 0.085	−0.350 ± 0.418	67
Chub	41.2 ± 2.1	0.435 ± 0.152	−0.205 ± 0.618	35
Dickie	37.1 ± 2.0	0.205 ± 0.076	−1.044 ± 1.599	52
Crosson	47.1 ± 1.0	0.279 ± 0.068	−1.132 ± 0.953	44
Gullfeather	36.9 ± 0.6	0.345 ± 0.032	0.742 ± 0.177	56

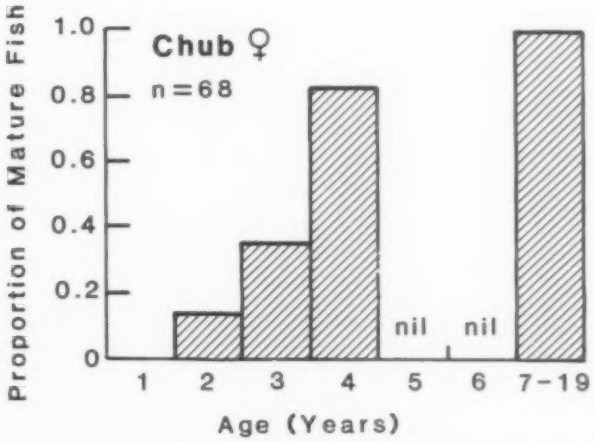


FIG. 5. Proportion of mature fish in each age class of female white suckers of Chub Lake origin. n = sample size; nil = no fish sampled of this age class.

G-test for this purpose (Zar 1984, p. 71) because data of this sort often have low frequencies or empty cells which bias many other tests adversely. For example, to test for a significant difference between males and females of the same population, a three-dimensional ($n \times 2 \times 2$) contingency table is first set up. The N rows are the number of age classes (or length intervals), the two columns refer to females and males, and the two layers (or tiers) are the number of immature and mature fish. If this test proves that a significant difference exists, then differences between specific age classes can be tested using a 2 × 2 contingency table. The Yates correction for continuity for 2 × 2 tables should be applied under certain conditions which have been outlined in Zar (1984, p. 72). Repetitive testing using either of these two methods within a single experimental design, however, may lead to falsely declaring a significant difference between two estimates of age at maturity, i.e. a type I error. Appropriate adjustments exist, one being to estimate the realistic probability of a type I error for each two-sample test (Trippel and Hubert 1990). For example, when using the Benferroni technique, one would carry out each individual test at the level $0.05/n$, when n ages at maturity are compared.

Advantages and disadvantages exist for each of the six methods. The advantages of $Probit_{50}$ are that it is simiple to apply, it derives 95% confidence intervals, it derives estimates of age at maturity at proportions other than 50%, and besides being available in many statistical software packages, a large amount of supportive literature on this method already exists. Disadvantages of $Probit_{50}$ are that it does not apply well to type I and IV distributions, it does not consider sample size per age class, and it may produce similar estimates for different maturity distributions. The latter disadvantage, however, is inherent in all six methods. The advantages of MLM_{50} are that it produces sensible estimates for many types of distributions, it can derive 95% plausibility estimates (Welch and Foucher 1988), it provides an estimate of the rate of change from 0 to 100% maturity by calculating the arithmetic slope $\phi'(X_{0.5})$, and it is the only method that considers sample size of each age class in computations. Our finding that $Probit_{50}$ and MLM_{50} generated similar estimates was of interest, particularly because $Probit_{50}$ fails to account for the sample size of fish in each age class. The disadvantage of MLM_{50} is that it does not apply well to type I and IV distributions. The advantages of Reg_{50} are that it is simple to apply, produces high r^2 values for type II distributions, software on linear regression analysis is readily available, and it produces 95% confidence intervals. The disadvantages of Reg_{50} are that it does not consider sample size per age class and it does not apply well to type I and IV distributions. The advantages of Lysack's formula is that it is very simple to apply with

TABLE 7. Methods recommended (r) and not recommended (nr) for the estimation of onset of sexual maturation for four types of maturity distributions of white sucker. The von Bertalanffy method pertains only to the estimation of length at sexual maturity. Caution in using any single value is highlighted in Table 8 where nearly the same estimates were derived for distributions with markedly different compositions.

Type of distribution	$Probit_{50}$	Maximum likelihood method (MLM_{50})	50% by regression (Reg_{50})	Lysack	≥50% by observation ($Obs_{\geq 50}$)	von Bertalanffy l_t (where t = age at maturity)
I. Abrupt transition to maturity	nr	nr	nr	r[a]	r[a]	nr
II. Successive annual increases in the proportion of mature fish	r	r	nr	nr	nr	nr
III. Nonsuccessive annual increases in the proportion of mature fish	r	r	nr	nr	nr	nr
IV. Nonattainment of 100% maturity	nr	nr	nr	nr	nr	nr

[a]Lysack's formula and $Obs_{\geq 50}$ may be used for type I distributions that maintain a high proportion of maturity with increase in age or length.
[b]Caution should be used when analysing type III distributions that have a highly variable maturity pattern.

TABLE 8. Estimates of maturity derived by each method that were within 5% of one another. A description of each method is given in the Methods section.

Method employed	Distributions	Onset of maturity (range)
	Age at maturity (yr)	
$Probit_{50}$	Red Chalk females and Chub males	2.17–2.19
	Chub and Crosson females	3.20–3.26
MLM_{50}	Red Chalk and Chub males	2.18–2.20
	Chub and Crosson females	3.25–3.28
Reg_{50}	King, Crosson, and George females	3.63–3.74
	Chub and King males	2.38–2.40
Lysack	Chub and Crosson females	Two of 4.07
	Crosson, George, and Gullfeather males	3.46–3.60
	Chub and King males	2.78–2.88
$Obs_{\geq 50}$	Bigwind and Red Chalk females and males	Four of 1.0
	Chub, King, and Crosson females	Five of 4.0
	Crosson and George males	
	Length at maturity (cm)	
$Probit_{50}$	Red Chalk females and King males	24.0–24.3
	King and Chub females	28.4–28.5
MLM_{50}	George and Gullfeather males	30.8–31.4
	Chub and King males	24.5–25.1
Reg_{50}	King and Gullfeather females	29.9–30.4
Lysack	Crosson and George females	34.5–34.8
	Crosson and George males	30.9–31.5
$Obs_{\geq 50}$	Bigwind females and males	Two of 15.0
	Red Chalk females and males	Two of 19.0
von Bertalanffy	Dickie, George, and Chub females	32.2–32.8
	Crosson females and George males	35.9–36.2
	Chub males and King females	29.5–30.1

no computer assistance required and it yields representative values for some type I and III distributions. The disadvantages of Lysack's formula are that it does not consider weighting of age classes based on sample size, it overestimates values for type II and some type III distributions, it may produce uncharacteristically low or even negative values for type IV distributions, and it generates no confidence intervals. The advantages of $Obs_{\geq 50}$ are that it is very simple to apply and it yields suitable estimates for some type I distributions. The disadvantages of $Obs_{\geq 50}$ are that it does not use the sample size of each age class, it is very inconsistent among distributions, and it produces no confidence intervals. The advantage of the method using the

von Bertalanffy growth equation is that it permits simple conversion from age to length at maturity. The disadvantage of this method is that it depends on a suitable fit of the growth equation to age–length data and a representative value of t, age at maturity.

It is likely that our assessment of methods used to estimate age and length at sexual maturity for white suckers is applicable to studies of other iteroparous fishes that exhibit a similar pattern of plasticity in maturation. In all cases, we recommend that researchers document maturity distributions concurrently with estimates of maturity.

Acknowledgements

The authors are indebted to the Ontario Ministry of Natural Resources, Bracebridge and Sudbury, for permission to investigate the dynamics of these fish populations. We are grateful for a Natural Sciences and Engineering Research Council of Canada grant to H.H.H. and for an Alexander von Humboldt Fellowship to E.A.T. while at Limnologisches Institut, Universität Konstanz, Germany. The final stages of manuscript preparation were done at the Biological Station, St. Andrews, N.B. The authors thank D. W. Welch who kindly made available his computer program for the maximum likelihood method and we thank Y. Chen, D. A. Jackson, W. Lysack, I. Perry, and P. Ryan for their helpful comments on an earlier version of the manuscript.

References

BEAMISH, R. J. 1973. Determination of age and growth of populations of the white sucker (*Catostomus commersoni*) exhibiting a wide range in size at maturity. J. Fish. Res. Board Can. 30: 607–616.

BEAMISH, R. J., AND H. H. HARVEY. 1969. Age determination in the white sucker. J. Fish. Res. Board Can. 26: 633–638.

BOWERING, W. R. 1983. Age, growth, and sexual maturity of Greenland halibut, *Reinhardtius hippoglossoides* (Walbaum), in the Canadian northwest Atlantic. Fish. Bull. 81: 599–611.

CHALANCHUK, S. M. 1984. Aging a population of the white sucker, *Catostomus commersoni*, by the fin-ray method. Can. Tech. Rep. Fish. Aquat. Sci. 1321.

DIANA, J. S. 1983. Growth, maturation, and production of northern pike in three Michigan lakes. Trans. Am. Fish. Soc. 112: 38–46.

FINNEY, D. J. 1971. Probit analysis. Cambridge University Press, Cambridge.

FRASER, N. C., AND G. POWER. 1989. Influences of lake trout on lake-resident Arctic char in northern Quebec, Canada. Trans. Am. Fish. Soc. 118: 36–45.

GEEN, G. H., T. G. NORTHCOTE, G. F. HARTMAN, AND C. C. LINDSEY. 1966. Life histories of two species of catostomid fishes in Sixteen Mile Lake, British Columbia, with particular reference to inlet stream spawing. J. Fish. Res. Board Can. 23: 1761–1788.

GOTO, A. 1987. Life history variation in males of the river sculpin, *Cottus hangiongensis*, along the course of a river. Environ. Biol. Fishes 19: 81–91.

HUBERT, J. J. 1984. Bioassay. 2nd ed. Kendall/Hunt Publ. Co., Dubuque, IA.

HUTCHINGS, J. A., AND D. W. MORRIS. 1985. The influence of phylogeny, size and behaviour on patterns of covariation in salmonid life histories. Oikos 45: 118–124.

LEGGETT, W. C., AND J. E. CARSCADDEN. 1978. Latitudinal variation in reproductive characteristics of American shad (*Alosa sapidissima*): evidence for population specific life history strategies in fish. J. Fish. Res. Board Can. 35: 1469–1478.

LOGAN, C., E. A. TRIPPEL, AND F. W. H. BEAMISH. 1991. Thermal stratification and benthic foraging patterns of white sucker. Hydrobiologia. 213: 125–132.

LYSACK, W. 1980. 1979 Lake Winnipeg fish stock assessment program. Man. Dep. Nat. Resour. MS Rep. 80-30: 118 p.

MCFARLANE, G. A., AND W. G. FRANZIN. 1978. Elevated heavy metals: a stress on a population of white suckers (*Catostomus commersoni*) in Hamell Lake, Saskatchewan. J. Fish. Res. Board Can. 35: 963–970.

MUNKITTRICK, K. R., AND D. G. DIXON. 1989. Use of white sucker (*Catostomus commersoni*) populations to assess the health of aquatic ecosystems exposed to low-level contaminant stress. Can. J. Fish. Aquat. Sci. 46: 1455–1462.

NAMMACK, M. F., J. A. MUSICK, AND J. A. COLVOCORESSES. 1985. Life history of spiny dogfish off the northeastern United States. Trans. Am. Fish. Soc. 114: 367–376.

NELDER, J. A., AND R. MEAD. 1965. A simplex method for function minimization. Comput. J. 7: 308–313.

NIKOL'SKII, G. V. 1962. On some adaptations to the regulation of population density in fish species with different types of stock structure, p. 265–282. *In* E. D. LeCren and M. W. Holgate [ed.] The exploitation of natural animal populations. Blackwell Scientific Publications, Oxford.

RICHARDS, L. J., J. T. SCHNUTE, AND C. M. HAND. 1990. A multivariate maturity model with a comparative analysis of three lingcod (*Ophiodon elongatus*) stocks. Can. J. Fish. Aquat. Sci. 47: 948–959.

ROFF, D. A. 1988. The evolution of migration and some life history parameters in marine fishes. Environ. Biol. Fishes 22: 133–146.

SAS. 1988. SAS user's guide: statistics, version 6.02. SAS Institute Inc., Cary, NC. 584 p.

SCHAFFER, W. M., AND P. F. ELSON. 1975. The adaptive significance of variations in life history among local populations of Atlantic salmon in North America. Ecology 56: 577–590.

SCHNUTE, J. T., AND L. J. RICHARDS. 1990. A unified approach to the analysis of fish growth, maturity, and survivorship data. Can. J. Fish. Aquat. Sci. 47: 24–40.

SOKAL, R. R., AND F. J. ROHLF. 1981. Biometry. 2nd ed. Freeman and Co., New York, NY.

SPANGLER, G. R., N. R. PAYNE, J. E. BYRNE, H. A. REGIER, AND W. J. CHRISTIE. 1977. Responses of percids to exploitation. J. Fish. Res. Board Can. 34: 1983–1988.

STEARNS, S. C., AND R. E. CRANDALL. 1984. Plasticity for age and size at sexual maturity: a life-history response to unavoidable stress, p. 2–33. *In* G. W. Potts and R. J. Wooton [ed.] Fish reproduction: strategies and tactics. Academic Press, New York, NY.

STEARNS, S. C., AND J. C. KOELLA. 1986. The evolution of phenotypic plasticity in life-history traits: predictions of reaction norms for age and size at maturity. Evolution 40: 893–913.

TRIPPEL, E. A. 1984. Gonadal development and body growth in the white sucker, *Catostomus commersoni* (Lacépède), in a group of south-central Ontario lakes having a wide range in acidity and mean depth. M.Sc. thesis, University of Toronto, Toronto, Ont. 162 p.

TRIPPEL, E. A., AND H. H. HARVEY. 1987a. Reproductive responses of five white sucker (*Catostomus commersoni*) populations in relation to lake acidity. Can. J. Fish. Aquat. Sci. 44: 1018–1023.

1987b. Abundance, growth and food supply of white suckers (*Catostomus commersoni*) in relation to lake morphometry and pH. Can. J. Zool. 65: 558–564.

1989. Missing opportunities to reproduce: an energy dependent or fecundity gaining strategy in white sucker (*Catostomus commersoni*) Can. J. Zool. 67: 2180–2188.

1990. Ovarian atresia and sex ratio imbalance in white sucker (*Catostomus commersoni*). J. Fish Biol. 36: 231–239.

TRIPPEL, E. A., AND J. J. HUBERT. 1990. Common statistical errors in fishery research, p. 93–102. *In* J. Hunter [ed.] Writing for fishery journals. American Fisheries Society, Bethesda, MD.

WAIWOOD, K. G., AND M.-I. BUZETA. 1989. Reproductive biology of southwest Scotian Shelf haddock (*Melanogrammus aeglefinus*). Can. J. Fish. Aquat. Sci. 46(Suppl. 1): 153–170.

WELCH, D. W., AND R. P. FOUCHER. 1988. A maximum likelihood methodology for estimating length-at-maturity with application to Pacific cod (*Gadus macrocephalus*) population dynamics. Can. J. Fish. Aquat. Sci. 45: 333–343.

ZAR, J. H. 1984. Biostatistical analysis. 2nd ed. Prentice-Hall, Englewood Cliffs, NJ.

Cycling of Phosphatase Hydrolyzable Phosphorus in Streams[1]

R. L. Klotz

Department of Biological Sciences, State University of New York, Cortland, NY 13045, USA

Klotz, R. L. 1991. Cycling of phosphatase hydrolyzable phosphorus in streams. Can. J. Fish. Aquat. Sci. 48: 1460–1467.

The phosphorus fraction made available to organisms by the action of alkaline phosphatase, here termed phosphatase hydrolyzable phosphorus (PHP), was studied in central New York State streams. Annual mean PHP concentrations were <2.0 μg P·L^{-1} for each of the four streams studied and were low relative to concentrations for lentic systems from the literature. The PHP to soluble reactive phosphorus (SRP) ratio, a measure of the relative importance of PHP for aquatic organisms, was typically in the 0.09–1.00 range, indicating that PHP could supply a significant amount of P at certain locations. Laboratory sorption experiments with varying ionic strength solutions and with Ca^{2+} versus Na^{+} suggested that PHP was probably bound to sediments by a different mechanism than SRP, one probably mediated by the organic moiety. Fine-grained sediments higher in organic matter sorbed excess PHP from solution at a greater rate than coarse-grained sediments, but also released more into PHP-depleted solutions.

La fraction phosphore rendue disponible pour les organismes par l'action de la phosphatase alcaline, appelée ici phosphore hydrolyzable par la phosphatase (PHP), a été étudiée dans des cours d'eau du centre de l'État de New York. Les concentrations moyennes annuelles de PHP étaient de moins de 2,0 μg P·L^{-1} pour chacun des quatre cours d'eau étudiés, et elles étaient faibles par rapport aux concentrations des systèmes lentiques signalés dans la documentation. Le rapport PHP à phosphore réactif soluble (PRS), mesure de l'importance relative du PHP pour les organismes aquatiques, était habituellement compris dans la plage 0,09–1,00, ce qui indique que le PHP pourrait fournir une quantité significative de P à certains endroits. Des expériences de sorption en laboratoire à l'aide de solutions ioniques de concentrations diverses, et comparant des solutions de Ca^{2+} à des solutions de Na^{+}, suggéraient que le PHP était probablement lié aux sédiments par un mécanisme différent de celui du PRS, et dans lequel la partie organique de la molécule agit probablement comme intermédiaire. Les sédiments à grains fins contenant une plus forte proportion de matières organiques sorbaient l'excès de PHP à une plus grande vitesse que les sédiments à grains grossiers, mais ils libéraient aussi une plus grande quantité de PHP dans les solutions pauvres en cette substance.

Received July 6, 1990
Accepted February 20, 1991
(JA637)

Reçu le 6 juillet 1990
Accepté le 20 février 1991

Many aquatic organisms produce enzymes which hydrolyze organic phosphorus compounds, thereby making orthophosphate available for uptake (Cembella et al. 1984a, 1984b). The most widely studied of these enzymes in freshwaters are the alkaline phosphatases, which are capable of hydrolyzing various phosphomonoesters (PME's) (Feder 1973; Herbes 1974). PME's are compounds which have covalent bonds between an oxygen of the phosphate group and a carbon of the R group (Scharpf 1973); phosphatases cleave the O—P linkage (McComb et al. 1979). Since not all PME's may be hydrolyzed by nonspecific alkaline phosphatases (McComb et al. 1979), this paper will refer to those that are hydrolyzed as phosphatase hydrolyzable phosphorus (PHP).

Our understanding of the importance of phosphatases and PHP in freshwaters has mainly come from studies on lakes; data from streams are limited. Regeneration of orthophosphate by phosphatases was reported to dominate P cycling in some lakes, revealing that PHP was an important P source, especially to algae, in these systems (Currie 1986; Currie et al. 1986; Jansson et al. 1988). Evidence supporting the hypothesis that algae readily utilize organic P was provided from studies on a marine phytoplankter which processed added organic phosphate twice as rapidly as the same concentration of orthophosphate (Admiraal and Veldhuis 1987). In other lakes, investigators have concluded that the hydrolysis of complex P compounds by naturally occurring phosphatases provides insignificant amounts of P for algae (Lean 1973; Heath 1986; Boavida and Heath 1988). In streams, alkaline phosphatase activity in sediment microorganisms and algae can be induced under natural conditions (Klotz 1985a, 1985b), making PHP potentially important. However, the types and abundance of organic P compounds in lotic systems that may be hydrolyzed enzymatically have generally received limited attention (Segars et al. 1986; Mulholland et al. 1988).

There were three main objectives in my research on the importance of PHP in the lotic environment. One was to evaluate the techniques for measuring enzymatically hydrolyzable P compounds in streams. Another was to measure and compare the concentration of PHP relative to other P fractions. The third objective was to determine the behavior of PHP relative to soluble reactive phosphorus (SRP) with regard to sorption by and release from streambed sediments.

Study Area

Four streams in Cortland County (Fig. 1) were chosen to provide examples of lotic systems draining the two dominant watershed types in central New York State; watersheds at sites 1 and 3 were 95 and 97% agricultural, respectively, while those at sites 2 and 4f were 98 and 94% wooded, respectively. These

[1]Contribution No. 21 of the Hoxie Gorge Field Station.

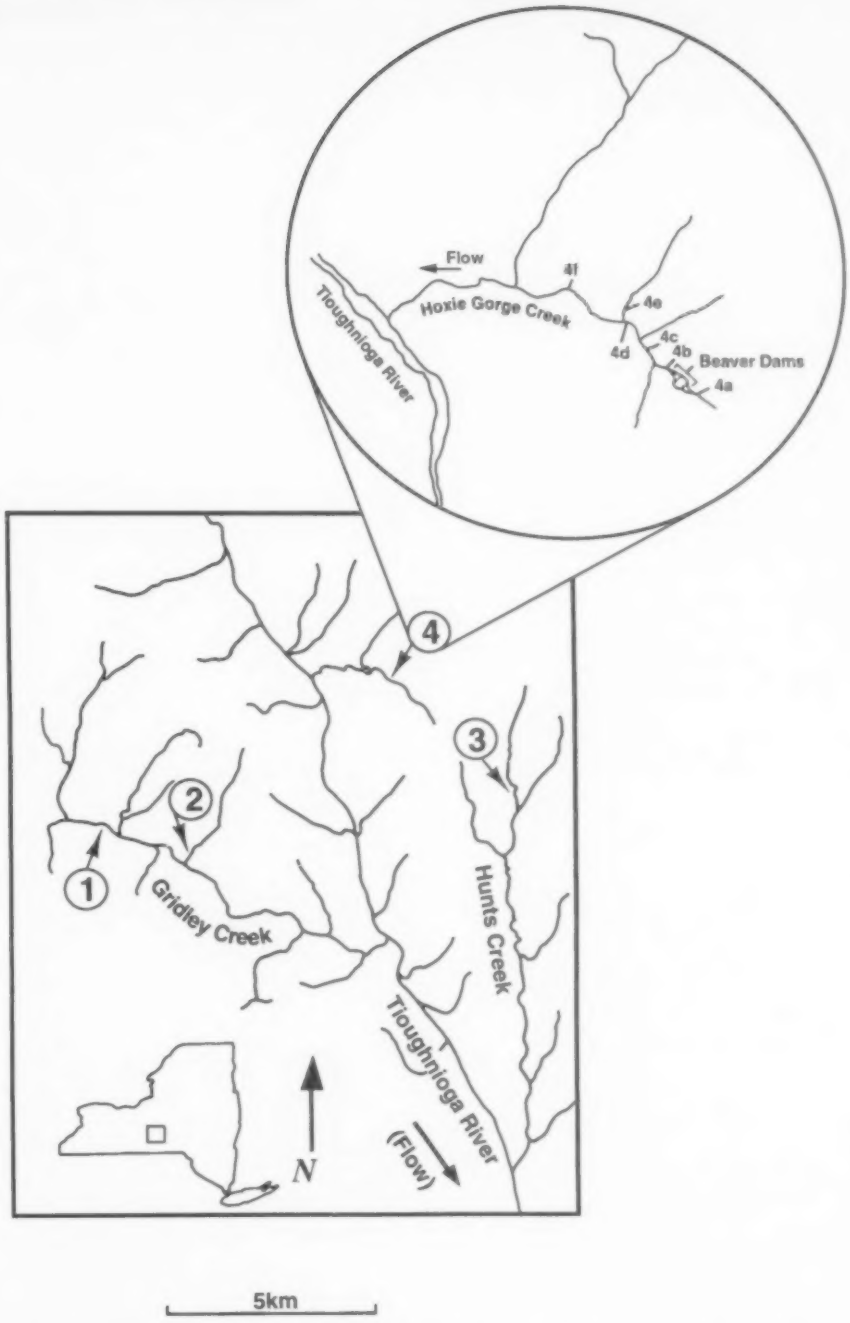


FIG. 1. Map of the sites located in Cortland County of New York State (lower left corner), USA.

four streams have been described previously (Klotz 1985a; site 4 in this previous paper is referred to as 4f here). Six sites (4a–4f) were established in Hoxie Gorge Creek (Fig. 1) to determine downstream trends, a stream reach previously described and shown to have streamwater SRP regulated by streambed sediments (Klotz 1988, 1991). Sediments along this reach became more coarse and decreased in organic matter downstream (Klotz 1988).

Methods

For all streamwater analyses in this study, collections were made in acid-cleaned 1-L polyethylene bottles and stored on

ice until returned to the laboratory. Samples were then immediately filtered (0.45-μm Millipore type HA, acid cleaned) and processed. PHP was measured by the monophosphate ester technique of Strickland and Solorzano (1966) and involved incubation at 30°C of 50 mL of filtered water sample with 1.0 mL of Tris buffer (0.1% w/v, pH 8.2; Trizma, Sigma Chemical Co.) and 1.0 mL (1 enzyme unit) of alkaline phosphatase solution. After the 2-h incubation, SRP was determined on the duplicate samples by the ascorbic acid method (APHA 1985) using a 10-cm cuvette. An increase in the P concentration determined in the enzyme-treated samples versus untreated samples analyzed for SRP represented the presence of PHP in the sample. Blanks and standards were prepared in duplicate in water purified by reverse osmosis to correct for possible P contaminants in the enzyme and buffer solutions. Alkaline phosphatase from bovine (calf) intestine (Sigma) was used throughout the study; alkaline phosphatase preparations from this source and *Escherichia coli* (Sigma) did not differ in their ability to hydrolyze compounds in Hoxie Gorge Creek, and neither hydrolyzed inositol hexaphosphate (IHP), a compound believed to dominate the organic P fraction in streams (Segars et al. 1986).

The technique of Strickland and Solorzano (1966), which utilized a commercially produced alkaline phosphatase capable of hydrolyzing a broad range of substrates, was compared with a technique which utilized enzymes naturally present in the water to measure enzymatically hydrolyzable P (EHP) (Chrost et al. 1986). In this second technique, 300 mL of filtered water was incubated at 30°C in 500-mL Erlenmeyer flasks with 3 mL of 1.0 M Tris buffer (pH 7.0) and 15 mL of chloroform to retard microbial activity. Some water samples were spiked with 20 μg $P \cdot L^{-1}$ of inositol monophosphate (IMP; myo-inositol 2-monophosphate di(cyclohexylammonium) salt; Sigma) and 20 μg $P \cdot L^{-1}$ of inositol hexaphosphate (IHP; phytic acid, sodium salt; Sigma). These compounds were chosen because they were believed to be important organic P compounds in streams (Segars et al. 1986). The spiked samples were run to determine if stream water had sufficient natural enzyme activity to hydrolyze excess PME's. Two 25-mL subsamples were removed from each flask at 2- to 3-d intervals and analyzed for SRP using a 10-cm cuvette (reagent volumes were one-half those used for a standard 50-mL sample by the ascorbic acid method (APHA 1985)). A measured increase in SRP in the water over the 7- to 14-d incubation period indicated both the presence of hydrolyzable P compounds in the water as well as natural enzymes capable of carrying out the hydrolysis. Samples were collected on 15 October 1986 from sites 4a and 4f and on 3 November 1986 from those two sites and from Casterline Pond (located 1 km north of Homer, NY, on Route 11). The pond sample was taken to compare the method in both the lentic and lotic habitat.

The levels of PHP and other P fractions were measured in two agricultural streams (sites 1 and 3) and in two wooded streams (sites 2 and 4f) during biweekly analyses between May 1984 and March 1985. These P fractions were also measured at six sites along Hoxie Gorge Creek during intermittent sampling between September 1985 and August 1987; most of the sampling dates were during the summer months. PHP was determined by the method of Strickland and Solorzano (1966) as previously described. Duplicate subsamples were analyzed for SRP by the ascorbic acid method and total soluble phosphorus (TSP) by treating filtered water samples with the persulfate digestion technique followed by SRP analysis (APHA 1985) using a 10-cm cuvette. Soluble unreactive phosphorus (SUP) was determined as the difference between TSP and SRP.

Various experiments were conducted to determine the interaction between PHP and streambed sediments. Since previous studies had shown greater SRP sorption by site 4a versus 4f sediments (Klotz 1988), experiments were done to see if this was also true for PHP. Two commercially available PHP compounds, glucose-1-phosphate (G-1-P; dipotassium salt; Sigma) and IMP, were utilized with site 4a and 4f sediments in analyses similar to zero equilibrium phosphate concentration (EPC_0) determinations (White and Beckett 1964; Taylor and Kunishi 1971). G-1-P was chosen because of its ubiquitous presence in cells as an intermediate in carbohydrate metabolism, and IMP was chosen because of its likely presence in streams (Segars et al. 1986). EPC_0 is the phosphate concentration in solution at which no net sorption or desorption of phosphate occurs by the sediments. These determinations were made using the technique developed by Klotz (1988) in which the incubating solution had a Ca concentration which simulated stream water. Briefly, duplicate sieved (2-mm mesh) fresh sediment subsamples (3 mL) were incubated the day of collection for 1 h at 20°C in 50 mL of 20 mg $Ca \cdot L^{-1}$ ($CaCl_2$) solution spiked with either G-1-P at 0, 5, and 10 μg $P \cdot L^{-1}$ or IMP at 0 and 20 μg $P \cdot L^{-1}$. Flasks were shaken vigorously for 5 s every 10 min during the incubation. The aqueous and sediment phases were separated by filtration through acid-cleaned 0.45-μm membrane filters (Millipore type HA). PHP (Strickland and Solorzano 1966) and SRP (APHA 1985) were determined as previously described. Also, in the same manner as the above measurements, P sorption was determined on sediments collected on 21 July 1986 as loss of PHP from IMP solutions of 10 and 20 μg $P \cdot L^{-1}$ and P release was determined on sediments collected on 24 July 1988 as the increase in PHP in the 0 μg $P \cdot L^{-1}$ (initial concentration) solution. Measured sediment subsamples were dried at 80°C to express EPC_0 and P sorption per unit dry weight. Size fractionation of Hoxie Gorge Creek sediments was done by sieving fresh samples through 2-mm mesh, drying at 80°C, and then sieving through 1.10-, 0.55- and 0.25-mm mesh. Size fractions were expressed as percent of total dry weight. Sediment organic content was estimated by weight loss of dried samples at 500°C in a muffle furnace.

Previous studies showed that streamwater ionic strength and Ca influenced the EPC_0 of Hoxie Gorge Creek sediments, a finding which revealed how the phosphate buffer mechanism operated (Klotz 1988). Experiments were conducted here to determine if the ionic strength and Ca concentration of the incubation solution influenced PHP sorption. Experiments were conducted with site 4b sediments collected on 20 April 1987 and with site 4f sediments collected on 10 April 1987. Ionic strength was adjusted to 0, 1.5, and 30 ($\times 10^{-3}$) with $CaCl_2$ or NaCl solutions. Incubations were conducted as previously described for the EPC_0 determinations.

Results

PHP concentrations determined by the technique of Strickland and Solorzano (1966) were similar to EHP concentrations determined by the method of Chrost et al. (1986) for unspiked water samples from sites 4a and 4f (Table 1). These data indicate that the natural enzymes dissolved in Hoxie Gorge Creek water were able to hydrolyze similar amounts of the organic P pool as was a commercially available broad-range alkaline phosphatase. However, results of enrichment experiments

TABLE 1. Enzyme hydrolyzable phosphorus (EHP) and phosphatase hydrolyzable phosphorus (PHP) at sites 4a and 4f. Units are $\mu g\ P \cdot L^{-1}$; mean (SE).

Site	Date	EHP	PHP
4a	15 October 1986	2.8 (0)	1.6 (0.2)
	3 November 1986	1.3 (0)	2.0 (0.2)
4f	15 October 1986	1.3 (0.1)	1.5 (0.1)
	3 November 1986	3.0 (0.1)	1.9 (0.4)

showed that there was both a spatial and temporal difference in the activity of these natural enzymes in Hoxie Gorge Creek water. This was shown by the fact that on 15 October 1986 there was a large increase in SRP in site 4a water enriched with IMP compared with unspiked site 4a water over the 7-d incubation period (Fig. 2), a result due to the release of SRP following hydrolysis of IMP by natural enzymes present in the water samples. Site 4f water enriched with IMP showed little increase in SRP (Fig. 2), indicating little enzymatic activity in the water. However, on 3 November 1986, more SRP was released from IMP following incubation in site 4f water versus site 4a (Fig. 3), but the most SRP was released from IMP-enriched pond water. These data indicated that the higher levels of dissolved natural enzymes necessary to hydrolyze the added IMP were not consistently present in stream water.

There was no SRP increase during the incubation period in IHP-enriched water from sites 4a and 4f (Fig. 2) and the pond (Fig. 3) compared with the unspiked samples from the respective sites. These data indicated that there were no natural dissolved enzymes present to hydrolyze IHP.

The annual mean concentrations for the P fractions are listed in Table 2 for sites 1–4f during 1984–85 and in Table 3 for sites 4a–4f during 1985–87. The annual mean concentrations of PHP ranged from 0.7 to 0.9 $\mu g\ P \cdot L^{-1}$ at sites 1–4f (Table 2) and from 0.9 to 1.9 $\mu g\ P \cdot L^{-1}$ at sites in Hoxie Gorge Creek (Table 3). PHP made significant contributions to the utilizable P pool when expressed relative to the low SRP values at certain sites; the PHP/SRP ratio ranged from 0.15 to 1.84 at the four streams studied (Table 2) and from 0.09 to 0.41 in Hoxie Gorge Creek (Table 3). The relatively high mean PHP/SRP ratios at sites 2 and 3 (Table 2) were due to one date at each site with very low SRP. With these dates eliminated for each site, the mean PHP/SRP ratio was 0.94 for site 2 and 0.65 for site 3.

Sediments at site 4a were finer grained than those at site 4f, and probably as a result exhibited a greater ability to sorb various compounds. Based on percent of total dry weight, 98.7% of sediments at site 4a passed through the finest mesh (0.25 mm) sieve, while at site 4f only 12.1% was less than 0.25 mm. At site 4a, 1.1% was in the 0.25- to 0.55-mm range and the remaining 0.2% was in the 0.55- to 1.1-mm range. At site 4f, 14.2% was in the 0.25- to 0.55-mm range, 35% was in the 0.55- to 1.1-mm range, and the remaining 38.7% was in the 1.1- to 2.0-mm range. The percent organic content (mean (SD)) during the PHP sorption and release experiments was 16.5 (2.3) at site 4a and 3.0 (0.1) at site 4f. Site 4a sediments sorbed both G-1-P and IMP to a greater extent than did site 4f sediments at all temperatures (Table 4), indicating that similar results may occur throughout the year. PHP release was greater for site 4a versus 4f sediments (Table 4). The EPC_0's determined with KH_2PO_4, G-1-P, and IMP in the incubating medium were always lower at site 4a versus 4f (Table 5), indicating that one would expect lower PHP concentrations at site 4a versus 4f if sediments were the dominant controlling factor of PHP levels.

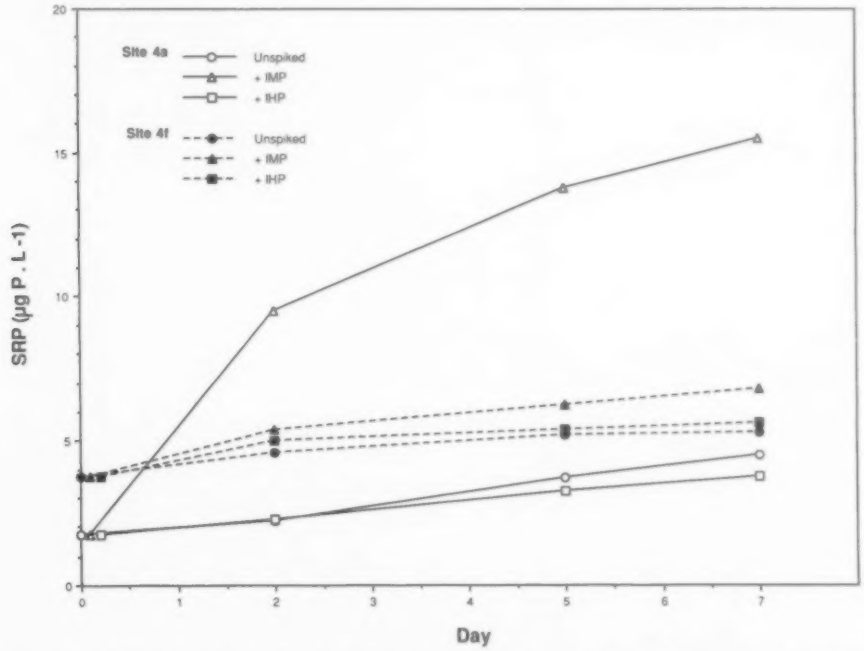


FIG. 2. Soluble reactive phosphorus (SRP) produced by hydrolysis of inositol monophosphate (IMP) and inositol hexaphosphate (IHP) by natural enzymes in stream water from sites 4a and 4f collected on 15 October 1986. SD bars were too small to show on this scale.

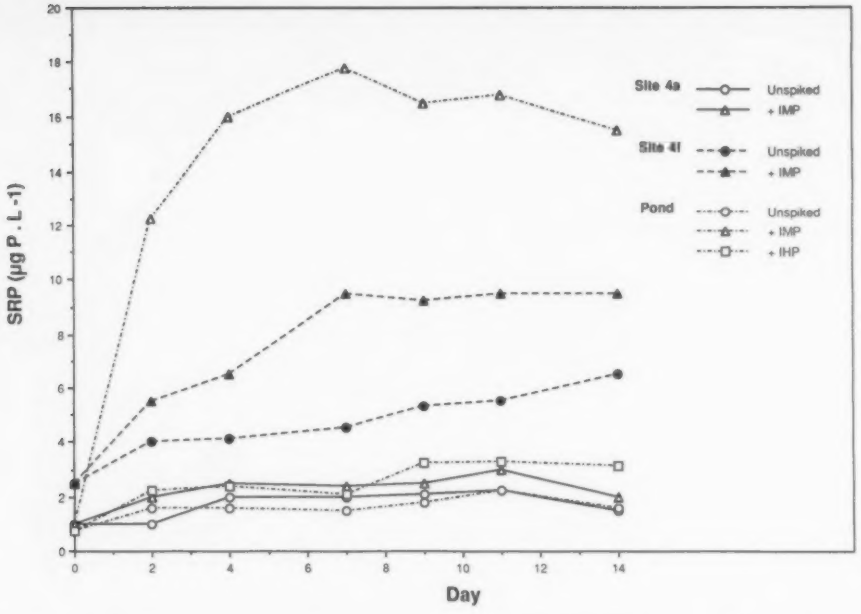


FIG. 3. Soluble reactive phosphorus (SRP) produced by hydrolysis by natural enzymes of inositol monophosphate (IMP) in water from sites 4a and 4f and of IMP and inositol hexaphosphate (IHP) in water from Casterline Pond collected on 3 November 1986. SD bars were too small to show on this scale.

TABLE 2. Soluble reactive phosphorus (SRP), phosphatase hydrolyzable phosphorus (PHP), total soluble phosphorus (TSP), and soluble unreactive phosphorus (SUP) at sites 1–4f from 22 May 1984 to 28 March 1985.

P fraction	Site 1	Site 2	Site 3	Site 4f
SRP[a] ($n = 17$)	2.1 (2.2)	1.0 (0.5)	2.4 (2.3)	5.4 (2.3)
PHP[a] ($n = 17$)	0.8 (0.6)	0.7 (0.5)	0.9 (0.7)	0.7 (0.4)
TSP[a] ($n = 17$)	5.3 (5.1)	2.8 (1.9)	6.9 (5.8)	7.8 (3.3)
SUP[a] ($n = 17$)	3.3 (3.2)	1.8 (1.7)	4.5 (4.0)	2.4 (1.6)
PHP/SRP[b] ($n = 17$)	0.98 (1.27)	1.71 (3.28)	1.84 (4.80)	0.15 (0.08)

[a]Units are µg P·L^{-1}; mean (SD).
[b]Mean (SD).

TABLE 3. Soluble reactive phosphorus (SRP), phosphatase hydrolyzable phosphorus (PHP), total soluble phosphorus (TSP), and soluble unreactive phosphorus (SUP) at sites 4a–4f along Hoxie Gorge Creek.

P fraction	Site 4a	Site 4b	Site 4c	Site 4d	Site 4e	Site 4f
SRP[a]	4:4 (1.7)	8.1 (3.5)	9.0 (2.7)	10.6 (2.5)	11.4 (3.1)	8.8 (3.8)
n	16	16	6	13	13	19
PHP[a]	1.5 (0.8)	1.9 (2.3)	1.7 (1.6)	1.2 (1.4)	0.9 (0.9)	1.3 (1.1)
n	16	16	6	13	13	19
TSP[a]	14.8 (7.7)	21.1 (10.9)	16.7 (5.6)	15.4 (4.8)	14.7 (7.2)	11.9 (4.5)
n	15	16	6	13	13	16
SUP[a]	10.2 (7.3)	13.0 (8.8)	7.8 (4.2)	4.9 (3.3)	3.4 (5.6)	3.3 (3.2)
n	15	16	6	13	13	16
PHP/SRP[b]	0.41 (0.31)	0.25 (0.23)	0.22 (0.20)	0.11 (0.09)	0.09 (0.09)	0.19 (0.20)
n	16	16	6	13	13	19

[a]Units are µg P·L^{-1}; mean (SD).
[b]Mean (SD).

Since increased ionic strength and greater cation charge were known to influence sorption of SRP, experiments were done to determine if similar effects occurred for PHP compounds. When the ionic strength of the incubating solution was increased from 0 to 30 ($\times 10^{-3}$) with either $CaCl_2$ or NaCl, there was no significant effect on IMP sorption by site 4b and 4f sediments (Table 6). There also was no significant difference between the effect of Ca^{2+} versus Na^{+} in the solution at equivalent ionic strengths (30×10^{-3}). These results indicate that PHP compounds interact with sediments in a different manner than SRP.

Discussion

Technique

The PHP measurements (Tables 2 and 3) made by the Strickland and Solorzano (1966) method were likely an accurate measure of that P which can be made available to the stream organisms by natural enzymatic hydrolysis. The PHP technique using a commercially available broad-range alkaline phosphatase was able to hydrolyze a similar amount of organic

TABLE 4. Sorption of inositol monophosphate (IMP) and release of phosphatase hydrolyzable phosphorus (PHP) versus temperature for sites 4a and 4f. Units are μg P·g sediment^{-1} sorbed or released during a 1-h incubation. Sorption experiments were conducted in solutions with initial IMP concentrations of 10 and 20 μg P·L^{-1}. Values are mean (SD).

Temp. (°C)	Site	IMP sorption 10 μg P·L^{-1}	IMP sorption 20 μg P·L^{-1}	PHP release
0	4a	0.38 (0.00)	1.0 (0.1)	0.20 (0)
	4f	0.01 (0.00)	0.04 (0.03)	0.04 (0.01)
10	4a	0.36[a]	0.93 (0.01)	0.17 (0.00)
	4f	0.01 (0.01)	0.06 (0.01)	0.04 (0.00)
25	4a	0.36 (0.02)	0.91 (0.05)	0.28 (0.03)
	4f	0.02 (0.00)	0.07 (0.01)	0.04 (0.01)

[a]One datum only.

TABLE 5. Zero equilibrium phosphorus concentrations (EPC_0) for sites 4a and 4f determined using KH_2PO_4, glucose-1-phosphate (G-1-P), and inositol monophosphate (IMP). Units are μg P·L^{-1}; mean (SD).

P source	EPC_0 Site 4a	EPC_0 Site 4f
KH_2PO_4[a]	0.4 (0.3)	7.1 (0.1)
G-1-P[a]	1.4 (0.5)	5.3 (1.5)
IMP[b]	2.1 (0.6)	11.3 (5.1)

[a]Determined 11 July 1986.
[b]Determined 21 July 1986.

TABLE 6. Effect of ionic strength and $CaCl_2$ and NaCl on inositol monophosphate (IMP) sorption by site 4b and 4f sediments. Units are μg P·g sediment^{-1} sorbed; mean (SD).[a,b]

Dissolved cation (mg·L^{-1})	Ionic strength (× 10^{-3})	Site 4b[c]	Site 4f[d]
0	0	0.73 (0.01)	0.12 (0.01)
Ca^{2+}, 400	30	0.76 (0.01)	0.07 (0.01)
Na^+, 690	30	0.65 (0)	0.04 (0.01)

[a]Initial IMP concentration was 15 μg P·L^{-1}.
[b]No significant difference in sorption was found between ionic strengths or between cations as determined by a *t*-test.
[c]Collected and analyzed 20 April 1987.
[d]Collected and analyzed 10 April 1987.

P compounds (Table 1) as the EHP technique (Chrost et al. 1986). The techniques were also similar in that IHP, a compound of likely quantitative importance in streams (Segars et al. 1986), was not hydrolyzed by either method.

The fact that much of the added IMP was not hydrolyzed by natural enzymes in stream water (Fig. 2 and 3) indicates that the technique of Chrost et al. (1986) may underestimate the streamwater concentration of hydrolyzable P compounds when the natural concentration is greater than that found here. It is not known whether the spatial and temporal variability in the activity of IMP hydrolyzing enzymes in stream water (Fig. 2 and 3) was due to discharge changes affecting dilution or to changes in enzyme production by the stream organisms. The greater hydrolysis of IMP by natural enzymes in the pond sample relative to the stream sample (Fig. 3) suggests that substantially lower dilution effects or greater enzyme production may characterize P cycling by hydrolytic enzymes in lentic versus lotic habitats. Enzymatic activity tightly associated with the cell walls of periphyton (Kuenzler and Perras 1965; Berman 1970) may be a more accurate measure of functional phosphatase activity in streams than that dissolved in the water, since dissolved phosphatase is lost by transport downstream.

The fact that the PME IHP (phytic acid; Scharpf 1973) was not hydrolyzed by broad-range phosphatases (calf intestinal and bacterial) reveals that caution must be used when interpreting the results of the Strickland and Solorzano (1966) technique. Phytase hydrolyzable organic P compounds (probably most of which were IHP or related compounds) were found to be quantitatively important in two lakes, with concentrations ranging from 1.1 to 4.0 μg P·L^{-1} (Herbes et al. 1975). Preliminary analyses from one date in April 1990 found streamwater phytase hydrolyzable P concentrations in this same range in Hoxie Gorge Creek (R. L. Klotz unpubl. data). Others have also suggested that IHP is a relatively abundant organic P compound in streams (Segars et al. 1986). IHP may be found at relatively high concentrations in water bodies because of its unavailability to broad-range alkaline phosphatases, natural enzymes (Fig. 2 and 3), and algae (Gibson and Whitton 1987). In waters in which IHP is an important component of the organic P pool, measurement techniques utilizing the broad-range alkaline phosphatases used in this study would lead to a serious underestimation of the true PME concentration. Also, calf intestine alkaline phosphatase has been shown to hydrolyze organic and inorganic polyphosphates as well as simple PME's (Morton 1955; Fernley and Walker 1967), a result which could lead to an overestimation. For the above reasons, I have used the term phosphatase hydrolyzable phosphorus (PHP) instead of PME to operationally define those organic P compounds hydrolyzed by the broad-range alkaline phosphatases of the Strickland and Solorzano (1966) technique.

Streamwater P Concentrations

The levels of streamwater PHP found here (Tables 2 and 3) show that this P source is important for sites with low SRP. This conclusion can be made because others have shown that P is a likely limiting nutrient in streams (e.g. Elwood et al. 1981; Stockner and Shortreed 1978) and that very low levels of P can influence specific growth rates of stream periphyton (Bothwell 1988). PHP may be functionally more important than the quantitative comparisons provided here, since studies on one phytoplankter showed that it processed organic P twice as rapidly as orthophosphate (Admiraal and Weldhuis 1987).

PHP may have provided a larger contribution to the utilizable P pool than the simple comparisons with SRP data indicated (Tables 2 and 3). This is because the SRP technique likely measured more than just orthophosphate (Rigler 1968; Downes and Paerl 1978; Stainton 1980; Tarapchak 1983), and the SRP values reported here may therefore have represented an overestimate of the true directly available phosphate concentration.

The rate of utilization of PHP is probably a better measure of its ecological importance than the concentration of PHP in the water. Jansson et al. (1988) postulated that the rate of substrate supply, rather than phosphatase activity, limits enzymatic phosphate regeneration. Therefore, low levels of substrate (PHP) may indicate that this source of P is being rapidly utilized by organisms. It remains to be seen if rapid utilization explains the low concentration of PHP found in these streams.

The concentration of PHP compounds has typically been found to be higher in lentic systems than the range of means (0.7–1.9 μg $P \cdot L^{-1}$) found for stream sites in this study (Tables 2 and 3). Levels in an acid bog lake ranged from 2.9 to 66.2 μg $P \cdot L^{-1}$, with a mean of 21.7 μg $P \cdot L^{-1}$, as determined by acid phosphatase digestion (Cotner and Heath 1988). In the surface layer of Lake Barato in central Hokkaido, Japan, hydrolyzable dissolved organic P (determined using alkaline phosphatases isolated from three algae) ranged from 2.2 to 61.4 μg $P \cdot L^{-1}$ (Hino 1988). The mean concentrations from five aquatic systems studied in Ohio ranged from 4.8 to 14.8 μg $P \cdot L^{-1}$ (Heath 1986), while in a eutrophic reservoir, lake PHP never exceeded 3 μg $P \cdot L^{-1}$ (Francko 1984). Perhaps the low PHP levels of lotic versus lentic systems result from differences in the source of the organic P. Sediments may be a more important source of organic P in streams like the ones studied here, while phytoplankton are likely to be a more important source in lakes. Hino (1988) showed that sediments had a lower percentage (relative to SUP) of PHP (20%) than did phytoplankton (>74%).

PHP Interaction with Sediments

Previous studies on SRP dynamics in Hoxie Gorge Creek provided a basis upon which to compare the behavior of PHP. Sediments were shown to regulate streamwater SRP at sites 4a–4f (Klotz 1988); those at site 4a maintained a lower streamwater SRP concentration (had a lower EPC_0) than site 4f sediments. For PHP, higher sorption rates (Table 4) and lower EPC_0 values (Table 5) for site 4a versus 4f sediments did not result in lower streamwater PHP at site 4a versus 4f (Table 3). This is in contrast with the EPC_0 measurements using KH_2PO_4 (Table 5) which did predict the downstream increase in SRP from site 4a to 4f (Table 3), a finding shown to be due to geochemical differences in the streambed sediments (Klotz 1988) and their effect on the phosphate buffer mechanism (Froehlich 1988). Also, the EPC_0 values were considerably higher than streamwater PHP at site 4f (Tables 3 and 5). Since EPC_0 using G-1-P and IMP did not accurately estimate downstream changes in and concentrations of streamwater PHP, it may be concluded that the phosphate buffer mechanism was not a major determinant of PHP as it was for SRP. Other instream processes not associated with sediments (e.g. uptake by periphyton on cobbles) or allochthonous inputs (e.g. springs, interflow) were perhaps more important in controlling PHP.

Although the overall total sorption of P at sites 4a and 4f was similar for SRP versus the PHP compounds studied (EPC_0 was lower for site 4a versus 4f using PHP compounds (Table 5) as well as SRP (Klotz 1988, 1991)), there were differences in behavior between the two P types. Previous studies (Klotz 1988) showed that the EPC_0 for SRP decreased as ionic strength increased, and at a given ionic strength, divalent cations influenced EPC_0 to a greater extent than monovalent cations, a behavior similar to soils (Traina et al. 1986). However, IMP did not respond in the same manner as SRP, for IMP sorption did not increase with ionic strength (Table 6), nor was there a difference in effect due to monovalent versus divalent cations at a given ionic strength for either site (Table 6). These data indicated that the organic moiety, not just the phosphate group, probably played a role in the sorption of the organic P compounds tested, a conclusion also reached by Shang et al. (1990).

Sediment size influenced sorption of IMP and G-1-P in a similar way as it did for SRP (Klotz 1988); fine-grained sediments from site 4a had a greater capacity for P sorption during the 1-h incubations than the coarse-grained sediments from site 4f (Table 4). This differential sorption behavior may influence P cycling and retention, two processes which influence the productivity and persistence of stream biota (Newbold et al. 1982). In streams, nutrient cycling has been conceptualized as a spiralling process (Webster 1975) with spiralling length as an index (Newbold et al. 1981). Spiralling length is the distance a hypothetical nutrient molecule travels downstream to make one complete cycle from the water column through the biota and back again; a short spiralling length indicates rapid cycling and high retention. In a mountain stream, spiralling length was found to be dominated by travel distance in the water, and therefore the primary constraint on increased nutrient utilization was probably uptake from the water column (Newbold et al. 1983). A similar result was found for the sediments of the four streams of this study: P limitation of sediment organisms was found to be influenced by the P sorption capacity of the sediments; those that sorbed SRP more rapidly showed less P limitation (Klotz 1985a). The same conclusion may also hold for PHP. Streams with fine-grained sediments due to natural or man-made impoundments or to shallow gradients will sorb PHP more rapidly and will have shorter spiralling lengths than will streams with coarse-grained sediments. If biotic uptake rate is closely associated with sediment sorption capacity, then stream sediment size variation would be expected to influence the nutrient retentiveness and productivity of streambed sediments.

Acknowledgements

I thank J. Dykstra, A. Funk, C. O'Brien, B. Over, and P. Ventiquattro for assistance with the P determinations and R T. Heath and an anonymous reviewer for providing helpful suggestions on the manuscript. This research was supported by a grant to the author from the National Science Foundation (BSR-8500225).

References

ADMIRAAL, W., AND M. J. W. VELDHUIS. 1987. Determination of nucleosides and nucleotides in seawater by HPLC; application to phosphatase activity in cultures of the alga *Phaeocystis pouchetti*. Mar. Ecol. Prog. Ser. 36: 277–285.

AMERICAN PUBLIC HEALTH ASSOCIATION (APHA). 1985. Standard methods for the examination of water and wastewater. 16th ed. APHA, Washington, DC. 1268 p.

BERMAN, T. 1970. Alkaline phosphatases and phosphorus availability in Lake Kinneret. Limnol. Oceanogr. 15: 663–674.

BOAVIDA, M. J., AND R. T. HEATH. 1988. Is alkaline phosphatase always important in phosphate regeneration? Arch. Hydrobiol. 111: 507–518.

BOTHWELL, M. L. 1988. Growth rate responses of lotic periphytic diatoms to experimental phosphorus enrichment: the influence of temperature and light. Can. J. Fish. Aquat. Sci. 45: 261–270.

CEMBELLA, A. D., N. J. ANTIA, AND P. J. HARRISON . 1984a. The utilization of inorganic and organic phosphorus compounds as nutreints by eukaryotic microalgae: a multidisciplinary perspective: Part I. CRC Crit. Rev. Microbiol. 10: 317–391.

1984b. The utilization of inorganic and organic phosphorus compounds as nutrients by eukaryotic microalgae: a multidisciplinary perspective: Part II. CRC Crit. Rev. Microbiol. 11: 13–81.

CHROST, R. J., W. SIUDA, D. ALBRECHT, AND J. OVERBECK. 1986. A method for determining enzymatically hydrolyzable phosphate (EHP) in natural waters. Limnol. Oceanogr. 31: 662–667.

COTNER, J. B., AND R. T. HEATH. 1988. Potential phosphate release from phosphomonoesters by acid phosphatase in a bog lake. Arch. Hydrobiol. 111: 329–338.

CURRIE, D. J. 1986. Does orthophosphate uptake supply sufficient phosphorus to phytoplankton to sustain their growth? Can. J. Fish. Aquat. Sci. 43: 1482–1487.

CURRIE, D. J., E. BENTZEN, AND J. KALFF. 1986. Does algal–bacterial phosphorus partitioning vary among lakes? A comparative study of ortho-

phosphate uptake and alkaline phosphatase activity in freshwater. Can. J. Fish. Aquat. Sci. 43: 311–318.

DOWNES, M. J., AND H. M. PAERL. 1978. Separation of two dissolved reactive phosphorus fractions in lake water. J. Fish. Res. Board Can. 35: 1636–1639.

ELWOOD, J. W., J. D. NEWBOLD, A. F. TRIMBLE, AND R. W. STARK. 1981. The limiting role of phosphorus in a woodland stream ecosystem: effects of P enrichment on leaf decomposition and primary producers. Ecology 62: 146–158.

FEDER, J. 1973. The phosphatases, p. 475–508. *In* E. J. Griffith, A. Beeton, J. M. Spencer, and D. T. Mitchell [ed.] Environmental phosphorus handbook. John Wiley and Sons, New York, NY.

FERNLEY, H. N., AND P. G. WALKER. 1967. Studies on alkaline phosphatase. Biochemistry 104: 1011–1018.

FRANCKO, D. A. 1984. Relationships between phosphorus functional classes and alkaline phosphatase activity in reservoir lakes. J. Freshwater Ecol. 2: 541–547.

FROEHLICH, P. N. 1988. Kinetic control of dissolved phosphate in natural rivers and estuaries: a primer on the phosphate buffer mechanism. Limnol. Oceanogr. 33: 649–668.

GIBSON, M. T., AND B. A. WHITTON. 1987. Influence of phosphorus on morphology and physiology of freshwater *Chaetophora*, *Draparnaldia* and *Stigeoclonium* (Chaetophorales, Chlorophyta). Phycologia 26: 59–69.

HEATH, R. T. 1986. Dissolved organic phosphorus compounds: do they satisfy planktonic phosphate demand in summer? Can. J. Fish. Aquat. Sci. 43: 343–350.

HERBES, S. 1974. Biological utilizability of dissolved organic phosphorus in natural waters. Ph.D. thesis, University of Michigan, Ann Arbor, MI. 236 p.

HERBES, S. E., H. E. ALLEN, AND K. H. MANCY. 1975. Enzymatic characterization of soluble organic phosphorus in lake water. Science (Wash., DC) 187: 432–434.

HINO, S. 1988. Fluctuation of algal alkaline phosphatase activity and the possible mechanisms of hydrolysis of dissolved organic phosphorus in Lake Barato. Hydrobiologia 157: 77–84.

JANSSON, M., H. OLSSON, AND K. PETTERSSEN. 1988. Phosphatases: origin, characteristics and function in lakes. Hydrobiologia 170: 157–175.

KLOTZ, R. L. 1985a. Factors controlling phosphorus limitation in stream sediments. Limnol. Oceanogr. 30: 543–553.

1985b. Influence of light on the alkaline phosphatase activity of *Selenastrum capricornutum* (Chlorophyceae) in streams. Can. J. Fish. Aquat. Sci. 42: 384–388.

1988. Sediment control of soluble reactive phosphorus in Hoxie Gorge Creek, New York. Can. J. Fish. Aquat. Sci. 45: 2026–2034.

1991. Temporal relation between soluble reactive phosphorus and factors in stream water and sediments in Hoxie Gorge Creek, New York. Can. J. Fish. Aquat. Sci. 48: 84–90.

KUENZLER, E. J., AND J. P. PERRAS. 1965. Phosphatases of marine algae. Biol. Bull. 128: 271–284.

LEAN, D. R. S. 1973. Phosphorus dynamics in lake water. Science (Wash., DC) 179: 678–680.

MCCOMB, R. B., G. N. BOWERS, AND S. POSEN. 1979. Alkaline phosphatase. Plenum Press, New York, NY. 986 p.

MORTON, R. K. 1955. The substrate specificity and inhibition of alkaline phosphatase of cow's milk and calf intestinal mucosa. Biochem. J. 61: 232–240.

MULHOLLAND, P. J., R. A. MINEAR, AND J. W. ELWOOD. 1988. Production of soluble, high molecular weight phosphorus and its subsequent uptake by stream detritus. Verh. Int. Ver. Limnol. 23: 1190–1197.

NEWBOLD, J. D., J. W. ELWOOD, R. V. O'NEILL, AND A. L. SHELDON. 1983. Phosphorus dynamics in a woodland stream ecosystem: a study of nutrient spiralling. Ecology 64: 1249–1265.

NEWBOLD, J. D., J. W. ELWOOD, R. V. O'NEILL, AND W. VAN WINKLE. 1981. Measuring nutrient spiralling in streams. Can. J. Fish. Aquat. Sci. 38: 860–863.

1982. Nutrient spiralling in streams: implications for nutrient limitation and invertebrate activity. Am. Nat. 120: 628–652.

RIGLER, F. H. 1968. Further observations inconsistent with the hypothesis that the molybdenum blue method measures inorganic phosphorus in lake water. Limnol. Oceanogr. 13: 7–13.

SCHARPF, L. G. 1973. Transformations of naturally occurring organophosphorus compounds in the environment, p. 393–412. *In* E. J. Griffith, A. Beeton, J. M. Spencer, and D. T. Mitchell [ed.] Environmental phosphorus handbook. John Wiley and Sons, New York, NY.

SEGARS, J. E., R. A. MINEAR, J. W. ELWOOD, AND P. J. MULHOLLAND. 1986. Chemical characterization of soluble phosphorus forms along a hydrologic flowpath of a forested stream ecosystem. Environmental Sciences Division Publication No. 2658. Oak Ridge National Laboratory, Oak Ridge, TN. 116 p.

SHANG, C., P. M. HUANG, AND J. W. B. STEWART. 1990. Kinetics of adsorption of organic and inorganic phosphates by short-range ordered precipitate of aluminum. Can. J. Soil Sci. 70: 461–470.

STAINTON, M. P. 1980. Errors in molybdenum blue methods for determining orthophosphate in freshwater. Can. J. Fish. Aquat. Sci. 37: 472–478.

STOCKNER, J. G., AND K. R. SHORTREED. 1978. Enhancement of autotrophic production by nutrient addition in a coastal rainforest stream on Vancouver Island. J. Fish. Res. Board. Can. 35: 28–34.

STRICKLAND, J. D. H., AND L. SOLORZANO. 1966. Determination of monoesterase hydrolyzable phosphate and phosphomonoesterase activity in seawater. *In* H. Barnes [ed.] Some contemporary studies in marine science. Allen and Unwin, London.

TARAPCHAK, S. J. 1983. Soluble reactive phosphorus measurements in lake water: evidence for molybdate enhanced hydrolysis. J. Environ. Qual. 12: 105–108.

TAYLOR, A. W., AND H. M. KUNISHI. 1971. Phosphate equilibria on stream sediment and soil in a watershed draining an agricultural region. J. Agric. Food Chem. 19: 827–831.

TRAINA, S. J., G. SPOSITO, D. HESTERBERG, AND U. KAFKAFI. 1986. Effects of ionic strength, calcium, and citrate on orthophosphate solubility in an acidic, montmorillonitic soil. Soil Sci. Soc. Am. J. 50: 623–627.

WEBSTER, J. R. 1975. Analysis of potassium and calcium dynamics in stream ecosystems on three southern Appalachian watersheds of contrasting vegetation. Dissertation, University of Georgia, Athens, GA.

WHITE, R. E., AND P. H. T. BECKETT. 1964. Studies on the phosphate potentials of soils. Part 1 — The measurement of phosphate potential. Plant Soil 20: 1–16.

Predicting Fish Mercury Levels from Physical Characteristics of Boreal Reservoirs

Thomas A. Johnston[1]

Department of Zoology, University of Manitoba, Winnipeg, Man. R3T 2N2, Canada

and R. A. Bodaly and J. A. Mathias

Department of Fisheries and Oceans, Central and Arctic Region, Freshwater Institute, Winnipeg, Man. R3T 2N6, Canada

Johnston, T. A., R. A. Bodaly, and J. A. Mathias. 1991. Predicting fish mercury levels from physical characteristics of boreal reservoirs. Can. J. Fish. Aquat. Sci. 48: 1468–1475.

Reservoir formation has often resulted in increased fish mercury levels. Predicting the potential for increase prior to impoundment would be useful in future environmental impact assessment. We developed several linear models relating mercury burdens of northern pike (*Esox lucius*), walleye (*Stizostedion vitreum*), and lake whitefish (*Coregonus clupeaformis*) to physical characteristics of 21 lakes and reservoirs in the Churchill River diversion region of northern Manitoba. Ratios of flooded terrestrial area to water volume of the reservoir itself (within-lake effects) and of inflowing waters (upstream effects) were able to explain 76–84% of the variation in mean mercury burden. Upstream effects consistently accounted for more variation than within-lake effects. We tested these models using data from 18 Canadian lakes and reservoirs. Manitoba reservoirs generally fit the models well. The largest deviations of observed mercury levels from predicted mercury levels were for reservoirs of northern Quebec and Labrador. We attribute this to differences in the relative contributions of within-lake effects and upstream effects between reservoirs of this region and those used to build the models. Future models should refine the relative contributions of these two components for individual reservoirs.

La formation des réservoirs a souvent entraîné une augmentation des teneurs en mercure des poissons. La prévision de la possibilité d'une augmentation avant l'emmagasinement serait utile pour les activités futures d'évaluation des répercussions environnementales. Nous avons élaboré plusieurs modèles linéaires mettant en rapport les charges corporelles de mercure du grand brochet (*Esox lucius*), du doré (*Stizostedion vitreum*) et de la grande corrégone (*Coregonus clupeaformis*) avec les caractéristiques physiques de 21 lacs et réservoirs de la région du détournement de la rivière Churchill dans le nord du Manitoba. Les rapports des volumes d'eau et des superficies terrestres inondées du réservoir lui-même (effets observés à l'intérieur du lac) et des eaux entrant dans le lac (effets en amont) pouvaient expliquer de 76 à 84 % des variations de la charge corporelle moyenne de mercure. Les effets en amont représentaient plus de variations que les effets dans le lac. Nous avons testé ces modèles à l'aide de données de 18 lacs et réservoirs canadiens. Les données des réservoirs du Manitoba correspondent généralement bien aux résultats des modèles. Les déviations les plus importantes entre les teneurs en mercure observées et celles qui étaient prévues étaient celles des réservoirs du nord du Québec et du Labrador. Nous attribuons ceci aux différences entre les contributions relatives des effets à l'intérieur du lac et des effets en amont, qui sont observés entre les réservoirs dans cette région et ceux qui ont été utilisés pour construire les modèles. Les modèles éventuels devraient raffiner les contributions relatives de ces deux composantes de façon à tenir compte des réservoirs particuliers.

Received July 24, 1990
Accepted February 20, 1991
(JA660)

Reçu le 24 juillet 1990
Accepté le 20 février 1991

The problem of elevated mercury levels in reservoir fish populations has been recognized for some time (Abernathy and Cumbie 1977; Lodenius et al. 1983; Bodaly et al. 1984; Boucher et al. 1985). Typically, fish mercury concentrations rise within a few years of reservoir formation and then decline to preimpoundment levels. The maximum level to which fish mercury concentrations will rise varies among reservoirs and among the resident species. The decline phase is also quite variable. Some studies have suggested that the return to baseline concentrations may occur within 5 yr after impoundment (e.g. Abernathy and Cumbie 1977; Cox et al. 1979) whereas others, particularly those examining northern reservoirs, predict a very slow decline and that mercury levels may remain elevated for decades (e.g. Bodaly et al. 1984). Because of the human health risks and economic damage which can result from mercury contamination of fisheries, the ability to predict the potential contamination level prior to reservoir construction would be valuable for future environmental impact assessment. Our purpose was to construct simple models which predict fish mercury levels from the physical changes in the waterbody which are expected to accompany reservoir construction.

The chemistry of mercury in aquatic environments and the process of mercury accumulation in fish have both been studied extensively (for reviews see Beijer and Jernelöv (1979) and Huckabee et al. (1979)). The monomethyl mercuric ion (methylmercury), CH_3Hg^+, is the most readily accumulated and most poorly eliminated form of this element, and the majority of

[1]Mailing address: Department of Fisheries and Oceans, Central and Arctic Region, Freshwater Institute, Winnipeg, Man. R3T 2N6, Canada.

mercury in fish is in this state (Huckabee et al. 1979). The conversion of inorganic mercury to methylmercury (methylation) occurs by abiotic or microbial means (Beijer and Jernelöv 1979) but the microbial pathway is considered the most important (Berman and Bartha 1986). The mercury concentration of fish depends on the methylmercury concentration in the water (Huckabee et al. 1979; Rodgers and Beamish 1981) and a multitude of factors influencing uptake and/or clearance rates.

The flooding of terrestrial soils and vegetation during impoundment adds inorganic mercury and organic nutrients to the aquatic system, both of which can elevate microbial methylmercury production (Wright and Hamilton 1982). As a result, the rate of methylmercury production in the flooded regions of reservoirs is often much higher than in the unflooded regions of reservoirs or in natural lakes (Ramsey 1989). In mesocosm experiments designed to simulate the effects of impoundment, Hecky et al. (1987) found that the addition of various organic materials stimulated mercury accumulation in yellow perch (*Perca flavescens*) muscle whereas additions of inorganic mercury and inorganic nutrients did not. Assuming that the increase in methylmercury production is proportional to the amount of organic matter added to the system, one would expect to find a relationship between the extent of flooding (terrestrial area inundated) and the mercury content of reservoir fish.

Modelling fish mercury levels as a function of extent of flooding in reservoirs has been attempted previously with mixed results. Jones et al. (1986) attempted to model fish mercury concentrations from a series of 28 physical and chemical variables measured on Canadian reservoirs. In their analyses, variables related to extent of flooding generally explained very little of the variation in fish mercury concentrations ($R^2 < 20\%$) and the authors concluded that extent of flooding would not be a useful predictor variable by itself. Derksen and Green (1986) found significant rank correlations between fish mercury concentration and the percent increase in reservoir surface area following impoundment but found no significant relationships in unranked analyses.

We feel that these previous studies did not find strong relationships between fish mercury levels and the physical impact of impoundment because they failed to account for several sources of variation, particularly reservoir age and external inputs of methylmercury to the reservoirs. Our objective was to develop improved models which account for these sources of variation and which would be capable of predicting fish mercury levels from the physical impact of future impoundments.

Methods

Model Building

The data used to build our models were collected from lakes impacted by the Churchill River diversion in northern Manitoba. The diversion project rerouted 75% of the Churchill River flow from Southern Indian Lake south to the Nelson River and flooded many lakes along the diversion route (Newbury et al. 1984).

The final data set contained 21 lakes and reservoirs (Table 1). Among these were six unimpacted waterbodies which we treated as controls. The three basins of Southern Indian Lake corresponding to areas 4, 5, and 6 as outlined in Newbury et al. (1984) were treated as separate reservoirs. The interconnected nature of this sytem allows waterborne mercury to travel between some waterbodies. Methylmercury in any one reservoir could come from two possible sources: from the flooded area of the reservoir itself and from the flooded areas of reservoirs upstream. Control lakes experienced neither within-lake nor upstream flooding effects.

TABLE 1. Year of impact, present status, and position relative to the Churchill River system for the 21 lakes and reservoirs used to build models relating fish mercury content to physical impact.

Position and status	Lake/reservoir	Year of impact
Upper Churchill, unimpacted	Sisipuk	—
	High Rock	—
	Granville	—
Southern Indian Lake, flooded	Opachuanau	1976
	SIL Area 4	1976
	SIL Area 5	1976
	SIL Area 6	1976
Diversion route, flooded	Issett	1975
	West/Central Mynarski	1975
	Rat	1974
	Notigi	1974
	Wapisu	1977
	Macheewin	1977
	Osik	1977
	Footprint	1977
	Threepoint	1977
	Wuskwatim	1977
	Birch Tree	1977
Off diversion route, unimpacted	Assean	—
	Costello	—
	Gauer	—

The original physical measurements collected for each reservoir included increase in surface level, preimpoundment area, and postimpoundment area. Changes in surface level were obtained from Newbury et al. (1984) and Manitoba Hydro (Winnipeg, Man., unpubl. data). Pre- and postimpoundment surface areas for Southern Indian Lake were taken from Newbury et al. (1984). All other areas were estimated from 1 : 50 000 topographic maps using a Calcomp 9100 digitizer. Flooded area (FA) for each reservoir was estimated as the difference between pre- and postimpoundment surface areas. Total area (TA) was taken as the postimpoundment surface area. The sum of the flooded areas of all reservoirs and river stretches upstream of a given lake was termed the upstream flooded area (UFA). Upstream total area (UTA) was calculated as the total area of all upstream waterbodies which experienced some rise in water level. Some flooded basins of Southern Indian Lake lie upstream of both the diversion route reservoirs and lakes on the original Churchill River route and were therefore expected to export methylmercury down both paths. In this situation, the downstream contribution of the flooded area to each route was considered proportional to the percentage of the total Churchill flow which followed each route. Using the water budget of McCullough (1981), we estimated the relative proportions of flow down the lower Churchill and diversion routes to be 0.19 and 0.81, respectively.

The physical variables used in our analyses were change in surface level (RISE), percent flooding (PF), upstream percent flooding (UPF), flooded area to volume ratio (AVR), and upstream flooded area to volume ratio (UAVR). The variables RISE, PF, and AVR were chosen to represent within-lake effects whereas UPF and UAVR represented upstream effects. Percent flooding was calculated as the ratio of FA to TA within a reservoir:

$$PF = \frac{FA}{TA} \times 100.$$

Upstream percent flooding was calculated similarly using the measurements UFA and UTA:

$$\text{UPF} = \frac{\text{UFA}}{\text{UTA}} \times 100.$$

Both PF and UPF represented the influence of the flooded area relative to the total area. Since it was assumed that net methylmercury produced is proportional to flooded area, the numerators in these two ratios should represent the total methylmercury released into the system whereas the denominators represent the capacity of the system to dilute this input. Volume would be a better choice than area as a measurement of dilution. Volumes were available only for the basins of Southern Indian Lake and Opachuanau Lake (Newbury et al. 1984). However, we estimated volumes for the remaining reservoirs using the empirical formula of Schneider and Haedrich (1989):

$$V = (3.6 \times 10^{-6}) \times A^{1.32}$$

where V is volume (cubic kilometres) and A is area (hectares). Substituting TA and UTA into this equation gave estimates of reservoir volume (VOL) and upstream volume (UVOL), respectively. These were used to calculate the variables AVR and UAVR:

$$\text{AVR} = \frac{\text{FA}}{\text{VOL}}$$

$$\text{UAVR} = \frac{\text{UFA}}{\text{UVOL}}.$$

Although both of these variables had dimensions of length^{-1}, they were considered to be proportional to methylmercury concentration.

Fish mercury data for Southern Indian Lake were taken from Bodaly et al. (1988). Fish mercury data for all other lakes and reservoirs were obtained from a mercury database maintained by the Inspection Services Branch of the Department of Fisheries and Oceans, Central and Arctic Region. This database included fish sampled from commercial catches and various surveys carried out in northern Manitoba. All mercury analyses were conducted at the Freshwater Institute using the methods of Hendzel and Jamieson (1976). Northern pike (*Esox lucius*), walleye (*Stizostedion vitreum*), and lake whitefish (*Coregonus clupeaformis*) were chosen as representative species because they were common to almost all of the lakes and they were the most important species in northern fisheries.

A relationship between body size and mercury concentration has been noted for many fish populations (e.g. Scott and Armstrong 1972). Regressions of $\log_e$ mercury concentration on $\log_e$ fork length for fish from the reservoirs of this study were highly variable for all species by reservoir combinations and had low coefficients of determination (often <40%). Some of the variation in mercury concentration of a given species at a given length was probably due to differences in body mass, since concentration depends both on body burden (micrograms of mercury per fish) and fish weight. To reduce some of this variation, we chose to use total body burdens of mercury rather than concentrations. Mercury burden was estimated as the product of fish wet weight and mercury concentration. Regressions of $\log_e$ burden on $\log_e$ fork length were used to determine the predicted mean mercury burden (MERC) of 550-mm northern pike, 400-mm walleye, and 350-mm lake whitefish. These sizes roughly corresponded to the mean size of each species as calculated from the fish mercury data.

Plots of MERC versus time since impact were constructed for each species by lake/reservoir combination. The trends were variable but generally, mercury burden rose, peaked, and then declined slowly over time following impoundment. We chose to use peak mercury levels in our model. Levels were most stable from 4 to 8 yr postimpoundment for northern pike and walleye and from 2 to 8 yr postimpoundment for lake whitefish. The values of MERC used in building our models were estimated for each species by lake/reservoir combination from regressions of $\log_e$ mercury burden on $\log_e$ fork length using data pooled over these specified time periods.

The relationships between MERC and the physical variables were examined using standard regression techniques (Draper and Smith 1981). Separate models were built for each species. All models were fit using SAS statistical packages (SAS Institute Inc. 1985).

We examined one and two variable linear models of the forms

$$\text{MERC}_i = b_0 + b_1 X_1 + \epsilon$$

and

$$\text{MERC}_i = b_0 + b_1 X_1 + b_2 X_2 + \epsilon$$

where MERC_i is the predicted mean mercury burden of species i, X_1, and X_2 are physical variables, and b_0, b_1, and b_2 are fitted parameters. Variables representing within-lake effects were strongly correlated with each other as were variables representing upstream effects ($r \geq 0.88$). Correlations between within-lake and upstream variables were weaker ($r \leq 0.61$). For this reason, two variable models were only fit for the variable combinations of PF with UPF and AVR with UAVR. Sequential F-tests (Draper and Smith 1981) were conducted to assess the value of adding more than one variable to the linear models. In these tests the variable which gave the best fit in a one-variable model always entered the two-variable model first.

Model Testing

We tested our models using fish mercury data and physical data from 18 Canadian lakes and reservoirs from Saskatchewan, Manitoba, Quebec, and Labrador (Table 2).

Physical data were available from published sources for the Nelson River lakes and reservoirs (Green 1986), Cedar Lake (Green and Derksen 1980), Cookson Reservoir (Munro 1985), Smallwood Reservoir (Duthie and Ostrofsky 1975), and most of the James Bay reservoirs (Brouard 1988). All other physical data were estimated from topographic maps.

Fish mercury data for Manitoba and Quebec waters were obtained from the Department of Fisheries and Oceans, Central and Arctic Region, and Hydro-Québec (M. Laperle, Vice-présidence Environnement, Hydro-Québec, Montréal, P.Q., pers. comm.), respectively. Published raw data were also available for Cookson Reservoir (Waite et al. 1980; Munro 1985) and Smallwood Reservoir (Bruce et al. 1979). Fish mercury data were only available from 10 yr postimpoundment for Karsakuwigamak and Pemichigamau reservoirs and 10–13 yr postimpoundment for the Nelson River waterbodies. Small sample sizes for Cookson Reservoir walleye necessitated combining data from 3 and 7 yr postimpoundment. Apart from these exceptions, all waterbodies were sampled within the time periods specified by our models.

TABLE 2. Year of impact and geographical location for 18 lakes and reservoirs used to test models relating fish mercury content to physical impact.

Location	Lake/reservoir	Year of impact
Northern Manitoba, Churchill River Diversion	Karsakuwigamak	1975
	Pemichigamau	1975
	Partridge Breast	1976
	Northern Indian	1976
Northern Manitoba, Nelson River	Sipiwesk	1960
	Split	1960
	Stephens	1970
Central Manitoba, Saskatchewan River	Cedar	1964
Southern Saskatchewan, East Poplar River	Cookson	1976
Northern Quebec, James Bay Project	Caniapiscau[a]	1982
	Fontanges	1983
	Vincelotte	1983
	La Grande 4	1983
	La Grande 3	1981
	La Grande 2[a]	1979
	Opinaca[a]	1980
	Boyd–Sakami[a]	1980
Eastern Labrador, Churchill Falls Project	Smallwood	1971

[a]Data available for both preimpoundment and postimpoundment conditions.

Observed MERC values were plotted against predicted MERC values for both the model building and the test data sets to assess goodness of fit.

Results

All single variable models were able to account for a significant amount of variation in MERC ($P < 0.01$) (Table 3). Variables representing within-lake effects (RISE, PF, or AVR) accounted for 34–59% of the variation in MERC. None of these variables consistently explained more variation than the others. Upstream effects (UPF or UAVR) generally explained much more variation (66–76%) than within-lake effects. This was evident for all species. Coefficients of determination were generally improved by using UAVR instead of UPF, but this effect was less evident between AVR and PF.

Combining within-lake and upstream effects into two-variable models accounted for 69–84% of the variation in MERC (Table 4). The addition of within-lake effects (PF or AVR) as a second variable significantly improved the models for walleye (sequential F-test, $P < 0.005$) and lake whitefish ($P < 0.04$), but not for northern pike ($P > 0.15$). Two-variable models using area to volume ratio variables (AVR and UAVR) generally gave equal or larger coefficients of determination than models using percent flooding variables (PF and UPF). Therefore, in further analyses we examined only the two-variable area to volume ratio models (AVR and UAVR) for each species.

Plots of observed MERC versus predicted MERC for the model building data indicated that a linear model was adequate (Fig. 1). Residuals showed no indication of a more appropriate model.

Observed versus predicted plots for the test data showed much more scatter than those of the model building data (Fig. 2). The trend of observed values increasing with predicted values was much clearer for walleye and lake whitefish than for northern pike.

For each fish species, MERC values were grouped according to the type of impact that the test lakes and reservoirs experienced: within-lake effects only, upstream effects only, combined within-lake and upstream effects, and no effects (controls). When observed MERC values were plotted against predicted MERC values, a clear separation of fish from waterbodies with only within-lake impact and those with only upstream or combined effects was evident (Fig. 2). This was most evident for northern pike, less noticeable for lake whitefish, and least evident for walleye. This ranking may reflect the high importance placed on upstream effects relative to within-lake effects by the northern pike model (parameter ratio

TABLE 3. Results of regression analysis for single-variable linear models using data from the lakes and reservoirs of Table 1. b_0 and b_1 are fitted parameters representing mean baseline burdens (intercept) and slope, respectively. Predicted mean mercury burden (MERC) was the dependent variable. See text for definition of independent variables.

Species	Independent variable	b_0	b_1	F (df)	P	R^2
Northern pike	RISE	561.5	104.40	14.86 (1,18)	0.0012	0.45
	PF	565.0	15.70	11.60 (1,19)	0.0030	0.38
	AVR	577.3	9.45	9.71 (1,19)	0.0057	0.34
	UPF	537.1	36.70	36.65 (1,19)	<0.0001	0.66
	UAVR	462.8	67.76	60.87 (1,19)	<0.0001	0.76
Walleye	RISE	304.6	58.53	23.64 (1,17)	<0.0001	0.58
	PF	292.7	10.18	23.51 (1,18)	<0.0001	0.57
	AVR	282.4	6.57	25.17 (1,18)	<0.0001	0.58
	UPF	326.0	19.23	34.42 (1,18)	<0.0001	0.66
	UAVR	287.9	35.13	50.87 (1,18)	<0.0001	0.74
Lake whitefish	RISE	67.1	8.15	9.21 (1,13)	0.0096	0.41
	PF	60.1	1.60	14.96 (1,14)	0.0017	0.52
	AVR	55.5	1.12	19.80 (1,14)	0.0005	0.59
	UPF	57.1	3.28	29.75 (1,14)	<0.0001	0.68
	UAVR	51.3	5.74	28.29 (1,14)	<0.0001	0.67

TABLE 4. Results of regression analysis for two-variable linear models combining within-lake effects (PF or AVR) and upstream effects (UPF or UAVR) and using data from the lakes and reservoirs of Table 1. b_0, b_1, and b_2 are fitted parameters representing mean baseline burdens, within-lake contributions, and upstream contributions, respectively. Probability of a larger F-statistic was <0.0001 for all regressions. Predicted mean mercury burden (MERC) was the dependent variable. See text for definition of independent variables.

Species	Independent variables	b_0	b_1	b_2	F (df)	R^2
Northern pike	PF, UPF	462.7	5.80	30.86	20.34 (2,18)	0.69
	AVR, UAVR	439.5	1.29	64.00	29.48 (2,18)	0.76
Walleye	PF, UPF	243.4	5.94	13.48	32.06 (2,17)	0.79
	AVR, UAVR	221.3	3.38	25.64	44.38 (2,17)	0.84
Lake whitefish	PF, UPF	45.7	0.85	2.45	23.04 (2,13)	0.78
	AVR, UAVR	42.4	0.60	3.90	21.16 (2,13)	0.77

b_2:b_1 ≈ 50) compared with the lake whitefish and walleye models (b_2:b_1 ≈ 7). Fish in reservoirs with only within-lake effects tended to have higher MERC than predicted whereas those with some upstream effects often had lower MERC than predicted.

With some exceptions, lakes and reservoirs from northern Manitoba fell closer to the observed–predicted line than others, suggesting a possible geographic influence (Fig. 2). The most southerly reservoir, Cookson, had a much lower observed burden than predicted for walleye (the only species sampled). This was unusual considering that Cookson experienced only a within-lake impact. This too may be a geographic effect.

Discussion

Our data demonstrated a strong relationship between the physical impact of impoundment and the mercury content of fish in lakes and reservoirs of the Churchill River diversion region of northern Manitoba. Physical variables as simple as the rise in water level accounted for a significant amount of the variation in fish mercury levels. This is an important finding because it suggests that the level of contamination could be predicted from information available prior to reservoir construction. Models utilizing biological variables or water chemistry variables would require extensive postimpoundment sampling and would not be as useful for environmental impact assessment.

Previous attempts to model fish mercury levels based on physical impact examined only the extent of flooding within the reservoirs (Derksen and Green 1986; Jones et al. 1986). Our data demonstrated that fish mercury levels within a reservoir may be as strongly related to the physical impact in upstream waters as to the physical impact in the reservoir itself. The effect of flooding soils and vegetation may be transported far downstream.

The strength of our models may also be due to our choice of dependent variable. The mercury content of reservoir fish is not only a function of the extent of flooding but also of fish size and the time since flooding. Previous models accounted for the former but not the latter of these two covariates (Derksen and Green 1986; Jones et al. 1986). In the case of the data used to construct our models, fish mercury burdens often rose, peaked, and then declined slowly following impoundment. This is qualitatively consistent with the pattern predicted by the time trend models of Messier et al. (1985). Time trends have also been observed for the mercury concentration of northern pike in Finnish reservoirs (Verta et al. 1986). Therefore, a statement of the mercury content of reservoir fish must be qualified by both the sample date and fish size. Accounting for both of these covariates may have improved the fit of our models.

It would appear that the main effect of impoundment is to inundate the terrestrial materials which stimulate methylmercury production. Organic matter from the soil and vegetation has a greater efect on fish mercury content than inorganic mercury or nutrients (Hecky et al. 1991). Indicators of organic content have been linked with fish mercury levels in natural lakes (McMurtry et al. 1989) and reservoirs (Mannio et al. 1986; Verta et al. 1986). The increase in methylmercury production following impoundment is probably closely related to the quantity of organic matter inundated and therefore to the area flooded. Thus, physical variables such as area to volume ratios represent rough estimates of the methylmercury concentration in the system.

The remaining variation in fish mercury content which was not accounted for by our models could be due to a variety of factors. Water chemistry can modify the influence of impoundment by affecting methylmercury concentration and/or its uptake by fish. pH may influence both the production of methylmercury (Winfrey and Rudd 1990) and its partitioning between the water and sediment (Miller and Akagi 1979). Relationships between pH and fish mercury content have been established for Finnish reservoirs (Verta et al. 1986) and Ontario lakes (McMurtry et al. 1989). The rate of methylmercury uptake by fish is known to be influenced by calcium concentration (McFarlane and Franzin 1980) and water hardness (Rodgers and Beamish 1983). Climate, soil type, and vegetation type may also be important factors, as they influence the quantity and quality of organic matter added and its rate of decomposition. By building our models using reservoirs from the same geographic area, we may have reduced much of the unexplained variation due to these factors.

The large deviations of observed MERC from predicted MERC for test reservoir fish suggest that the relationships expressed by our models are not as strong for reservoirs in other geographic regions, or that these relationships are region specific. Generally, the closest agreements between test data and our models' predictions were for mercury burdens of fish from northern Manitoba reservoirs. Differences in water chemistry, soil, vegetation, and climate between northern Manitoba and other geographic regions represented in our test data set may account for some of the deviation from predicted mercury burdens for reservoirs outside of Manitoba. However, in addition to these factors, some of the deviation of test data from predicted values may be due to the static nature of the model. In particular, we feel the model has two flaws worth noting.

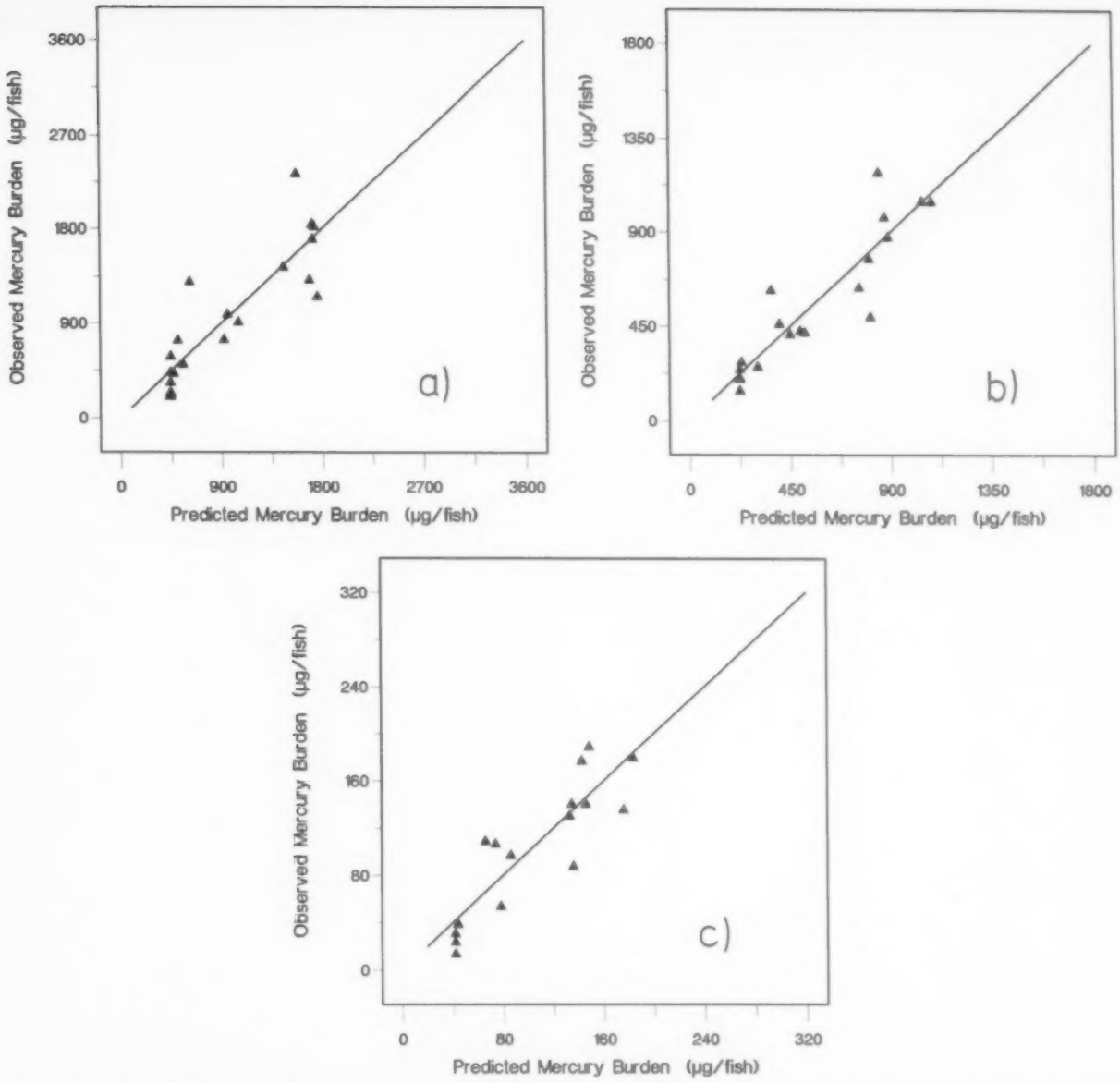


FIG. 1. Scatter plots of observed MERC versus predicted MERC for lakes and reservoirs of the model building data set (listed in Table 1). Predicted values were estimated from the two-variable (AVR and UAVR) models of Table 4. Plots are for (a) 550-mm northern pike, (b) 400-mm walleye, and (c) 350-mm lake whitefish. Note scale of axes differs for each species. Reference line indicates a 1:1 agreement between observed and predicted values.

First, we considered the effect of upstream flooding as independent of its distance from the reservoir. However, fish mercury levels in outflowing waters are often as high or higher than those in the reservoir itself over short distances and then gradually decline over longer distances. This pattern has been observed in the La Grande River below the LG2 reservoir (Brouard et al. 1989) and in the Churchill River below Smallwood Reservoir and the Churchill River below Southern Indian Lake (pers. obs.; data of this study). The decline in fish mercury with increasing distance would be expected, as demethylation and dilution reduce the methylmercury concentration of the water.

The second, and possibly more serious, problem with our model is the fact that within-lake and upstream variables are given the same relative importance (expressed quantitatively by the parameter ratio) for every reservoir. Thus, for our two-variable area to volume ratio models, upstream effects always influence mercury burdens more than within-lake effects by a factor of 7 for walleye and lake whitefish and by a factor of 50 for northern pike. However, the relative importance of each variable would be expected to vary from one reservoir to

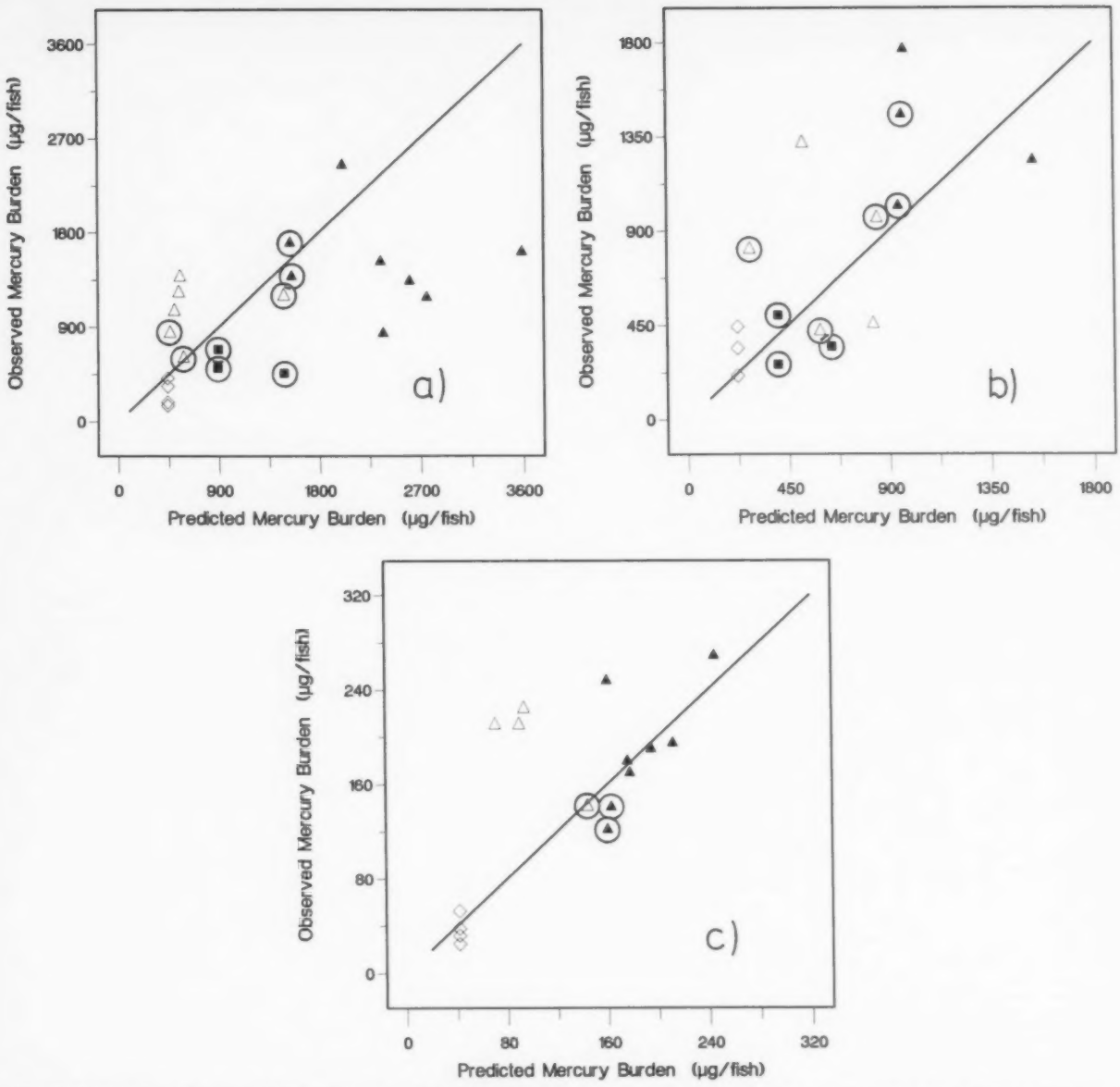


FIG. 2. Scatter plots of observed MERC versus predicted MERC for lakes and reservoirs of the test data set (listed in Table 2). Predicted values were estimated from the two-variable (AVR and UAVR) models of Table 4. Symbols represent various types of impact: upstream effects only (■), in-lake effects only (Δ), upstream and in-lake effects combined (▲), and controls (◇). Plots are for (a) 550-mm northern pike, (b) 400-mm walleye, and (c) 350-mm lake whitefish. Note scale of axes differs for each species. Reference line indicates a 1:1 agreement between observed and predicted values. Circled points represent reservoirs of northern Manitoba.

another, depending on hydrological conditions. Reservoirs of the test data set which differed greatly in structure from the model building reservoirs showed some of the largest deviations of observed from predicted mercury burdens. Reservoirs having extensive within-lake flooding but no upstream effects (e.g. Smallwood, Opinaca, and Caniapiscau) and reservoirs having extensive flooding both within and upstream (e.g. Boyd-Sakami) were not well represented in the model building data set. Consequently, our model predictions were often too low for the former group and too high for the latter group. This was most evident for the northern pike model (Fig. 2a).

Future attempts at improving the models developed in this study could follow several directions. However, we feel that methods of assessing the relative contributions of within-lake and upstream effects for each individual reservoir would improve these models the most. This would probably require additional hydrological information such as inflow rates, outflow rates, and more accurate estimates of reservoir volume. This information could be obtained prior to reservoir construction. Some means of accounting for variation due to water

chemistry, soil type, vegetation type, and climate may improve the models, although developing quantitative variables for these factors would be difficult.

Acknowledgements

We wish to thank Dave Green, Marilyn Hendzel, Pat Jones, Brian Korbaylo, Marcel Laperle, and Greg McCullough for providing data. Dave Schneider offered some helpful advice and Larry Dueck assisted with data transfer. Brigitte de March, John Rudd, and two anonymous referees kindly reviewed the manuscript and provided many useful criticisms. Funding was provided by a Natural Sciences and Engineering Research Council of Canada (NSERC) postgraduate scholarship to T. A. Johnston.

References

ABERNATHY, A. R., AND P. H. CUMBIE. 1977. Mercury accumulation by largemouth bass (*Micropterus salmoides*) in recently impounded reservoirs. Bull. Environ. Contam. Toxicol. 17: 595–602.

BEIJER, K., AND A. JERNELÖV. 1979. Methylation of mercury in aquatic environments, p. 203–210. *In* J. O. Nriagu [ed.] The biogeochemistry of mercury in the environment. Elsevier/North Holland Biomedical Press, Amsterdam, The Netherlands.

BERMAN, M., AND R. BARTHA. 1986. Levels of chemical versus biological methylation of mercury in sediments. Bull. Environ. Contam. Toxicol. 36: 401–404.

BODALY, R. A., R. E. HECKY, AND R. J. P. FUDGE. 1984. Increases in fish mercury levels in lakes flooded by the Churchill River diversion, northern Manitoba. Can. J. Fish. Aquat. Sci. 41: 682–691.

BODALY, R. A., N. E. STRANGE, AND R. J. P. FUDGE. 1988. Mercury content of fish in the Southern Indian Lake and Issett reservoirs, northern Manitoba, before and after Churchill River diversion. Can. Data Rep. Fish. Aquat. Sci. 706: v + 59 p.

BOUCHER, R., R. SCHETANGE, AND E. MAGNIN. 1985. Teneur en mercure des poissons des réservoirs La Grande 2 et Opinaca (Québec, Canada) avant et après la mise en eau. Rev. Fr. Sci. Eau 4: 193–206.

BROUARD, D. 1988. Réseau de suivi environmental du complexe La Grande, Phase I (1986): évolution du mercure dans la chair des poissons (secteur ouest du territoire). Rapport d'étape pour le service Études et Recherches écologiques, Direction Environnement, Hydro-Québec, Montréal, P.Q. 53 p.

BROUARD, D., C. DEMERS, R. LALUMIÈRE, R. SCHETAGNE, AND R. VERDON. 1989. Evolution of mercury levels in fish of the La Grande hydroelectric complex, Québec (1978–1989). Summary Report. Vice-présidence Environment, Hydro-Québec and Groupe Environnement Shooner Inc., Montréal, P.Q. 97 p.

BRUCE, W. J., K. D. SPENCER, AND E. ARSENAULT. 1979. Mercury content data for Labrador fishes, 1977–1978. Fish. Mar. Serv. Data Rep. 142: iv + 263 p.

COX, J. A., J CARNAHAN, J. DINUNZIO, J. MCCOY, AND J. MEISTER. 1979. Source of mercury in fish in new impoundments. Bull. Environ. Contam. Toxicol. 23: 779–783.

DERKSEN, A. J., AND D. J. GREEN. 1986. Total mercury concentrations in large fishes from lakes on the Churchill River diversion and Nelson River. Canada–Manitoba Agreement on the Study and Monitoring of Mercury in the Churchill River Diversion. Project 3.3. Mercury in Fish. Tech. Appendices to the Summary Report. Vol. 4. Manitoba Department of Natural Resources, Fisheries Branch, Winnipeg, Man. xi + 195 p.

DRAPER, N. R., AND H. SMITH. 1981. Applied regression analysis. 2nd ed. John Wiley and Sons, New York, NY. 709 p.

DUTHIE, H. C., AND M. L. OSTROFSKY. 1975. Environmental impact of the Churchill Falls (Labrador) hydroelectric project: a preliminary assessment. J. Fish. Res. Board Can. 32: 117–125.

GREEN, D. J. 1986. Summary of fish mercury data collected from lakes on the Rat–Burntwood and Nelson River systems, 1983–1985. Man. Dept. Nat. Res. Fish. Branch Manuscr. Rep. 86-06: 359 p.

GREEN, D. J., AND A. J. DERKSEN. 1980. The post-impoundment area and bathymetry of Cedar Lake, Manitoba. Man. Dep. Nat. Res. Fish. Branch Manuscr. Rep. 80-10: 16 p.

HECKY, R. E., R. A. BODALY, D. J. RAMSEY, AND N. E. STRANGE. 1991. Increased methylmercury contamination in fish in newly formed freshwater reservoirs. *In* T. F. W. Clarkson, T. Suzuki, and A. Imura [ed.] Advances in mercury toxicology. Plenum Press, New York, NY.

HECKY, R. E., R. A. BODALY, N. E. STRANGE, D. J. RAMSEY, C. ANEMA, AND R. J. P. FUDGE. 1987. Mercury bioaccumulation in yellow perch in limnocorrals simulating the effects of reservoir formation. Can. Data Rep. Fish. Aquat. Sci. 628: v + 158 p.

HENDZEL, M. R., AND D. M. JAMIESON. 1976. Determination of mercury in fish. Anal. Chem. 48: 926–928.

HUCKABEE, J. W., J. W. ELWOOD, AND S. G. HILDEBRAND. 1979. Accumulation of mercury in freshwater biota, p. 277–301. *In* J. O. Nriagu [ed.] The biogeochemistry of mercury in the environment. Elsevier/North Holland Biomedical Press, Amsterdam, The Netherlands.

JONES, M. L., G. L. CUNNINGHAM, D. R. MARMOREK, P. M STOKES, C. WREN, AND D. DEGRAFF. 1986. Mercury release in hydroelectric reservoirs. Canadian Electrical Association Report No. 185 G 399, Canadian Electrical Association, Research and Development, Montréal, P.Q. 156 p.

LODENIUS, M., A. SEPPÄNEN, AND M. HERRANEN. 1983. Accumulation of mercury in fish and man from reservoirs in northern Finland. Water Air Soil Pollut. 19: 237–246.

MANNIO, J., M. VERTA, P. KORTELAINEN, AND S. REKOLAINEN. 1986. The effect of water quality on the mercury concentration of northern pike (*Esox lucius*, L.) in Finnish forest lakes and reservoirs. Vesientutkimuslaitoksen Julk. 65: 32–43.

MCCULLOUGH, G. K. 1981. Water budgets for Southern Indian Lake, Manitoba, before and after impoundment and Churchill River diversion, 1972–1979. Can. MS Rep. Fish. Aquat. Sci. 1620: iv + 22 p.

MCFARLANE, G. A., AND W. G. FRANZIN. 1980. An examination of Cd, Cu, and Hg concentrations in livers of northern pike, *Esox lucius*, and white sucker, *Catostomus commersoni*, from five lakes near a base metal smelter at Flin Flon, Manitoba. Can. J. Fish. Aquat. Sci. 37: 1573–1578.

MCMURTRY, M. J., D. L. WALES, W. A. SCHEIDER, G. L. BEGGS, AND P. E. DIMOND. 1989. Relationship of mercury concentrations in lake trout (*Salvelinus namaycush*) and smallmouth bass (*Micropterus dolomieui*) to the physical and chemical characteristics of Ontario lakes. Can. J. Fish. Aquat. Sci. 46: 426–434.

MESSIER, D., D. ROY, AND R. LEMIRE. 1985. Réseau de surveillance écologique du complexe La Grande 1978–1984: évolution du mercure dans la chair des poissons. Société d'énergie de la Baie James. Direction Ingénierie et Environnement, Montréal, P.Q. 170 p.

MILLER, D. R., AND H. AKAGI. 1979. pH affects mercury distribution, not methylation. Ecotoxicol. Environ. Saf. 3: 36–38.

MUNRO, D. J. 1985. Report on mercury in Cookson reservoir. Environment Canada, Western and Northern Region, Water Quality Branch Report No. 85-02. 25 p.

NEWBURY, R. W., G. K. MCCULLOUGH, AND R. E. HECKY. 1984. The Southern Indian Lake impoundment and Churchill River diversion. Can. J. Fish. Aquat. Sci. 41: 548–557.

RAMSEY, D. J. 1989. Measurements of methylation balance in Southern Indian Lake and Granville Lake, Manitoba, and in Sokatisewin Lake, Saskatchewan, 1988. Environment Canada, Ecological Report Series No. 89-2, Northern Flood Agreement, Manitoba. 95 p.

RODGERS, D. W., AND F. W. H. BEAMISH. 1981. Uptake of waterborne methylmercury by rainbow trout (*Salmo gairdneri*) in relation to oxygen consumption and methylmercury concentration. Can. J. Fish. Aquat. Sci. 38: 1309–1315.

1983. Water quality modifies uptake of waterborne methylmercury by rainbow trout, *Salmo gairdneri*. Can. J. Fish. Aquat. Sci. 40: 824–828.

SAS INSTITUTE INC. 1985. SAS user's guide: statistics, version 5 edition. SAS Institute Inc., Cary, NC. 956 p.

SCHNEIDER, D. C., AND R. L. HAEDRICH. 1989. Prediction limits of allometric equations: a reanalysis of Ryder's morphoedaphic index. Can. J. Fish. Aquat. Sci. 46: 503–508.

SCOTT, D. P., AND F. A. J. ARMSTRONG. 1972. Mercury concentration in relation to size in several species of freshwater fishes from Manitoba and northwestern Ontario. J. Fish. Res. Board Can. 29: 1685–1690.

VERTA, M., S. REKOLAINEN, AND K. KINNUNEN. 1986. Causes of increased fish mercury levels in Finnish reservoirs. Vesientutkimuslaitoksen Julk. 65: 44–58.

WAITE, D. T., G. W. DUNN, AND R. J. STEDWILL. 1980. Mercury in Cookson reservoir. Saskatchewan Environment, Water Pollution Control Branch, Report No. 23: 19 p.

WINFREY, M. R., AND J. W. M. RUDD. 1990. Environmental factors affecting the formation of methylmercury in low pH lakes. Environ. Toxicol. Chem. 9: 853–869.

WRIGHT, D. R., AND R. D. HAMILTON. 1982. Release of methyl mercury from sediments: effects of mercury concentration, low temperature, and nutrient addition. Can. J. Fish. Aquat. Sci. 39: 1459–1466.

Interaction of Abiotic and Biotic Factors Influences Larval Fish Survival in an Oklahoma Stream

Bret C. Harvey[1]

Department of Zoology and Biological Station, University of Oklahoma, Norman, OK 73019, USA

Harvey, B. C. 1991. Interaction of abiotic and biotic factors influences larval fish survival in an Oklahoma stream. Can. J. Fish. Aquat. Sci. 48: 1476–1480.

Both abiotic and biotic factors affected larval fish in Baron Fork, Oklahoma. Nighttime drift rates were very high (up to 31 larvae/m^3) during normal flow. Censuses indicated that daytime abundances of larvae occupying pools were influenced significantly by the presence of juvenile and adult smallmouth bass (*Micropterus dolomieui*). Minnow larvae were less abundant in pools occupied by juvenile smallmouth bass and more abundant in pools with adult smallmouth bass. Experimental manipulation of adult bass supported the hypothesis that their presence benefits the larvae of other species, but pool type influenced this response. Differences between the effects of adult bass on the accumulation of larvae in main channel pools compared with side pools appeared to reflect the influence of drift. The benefit that adult bass provided the larvae of other species probably involved their impacts on juvenile bass and other small fishes, which may be the most significant predators of larval fish. The pattern of co-occurrence between adult bass and the larvae of other species in Baron Fork parallels results from lakes and smaller streams.

Les facteurs abiotiques et biotiques ont influé sur le comportement des larves de poissons à Baron Fork, Oklahoma. Les taux de dérive nocturne étaient très élevés (jusqu'à 31 larves/m^3) au cours de l'écoulement normal. Les recensements ont indiqué que les abondances diurnes de larves occupant des bassins étaient influencées de façon significative par la présence de juvéniles et d'adultes d'achigans à petite bouche (*Micropterus dolomieui*). Les larves de fretin étaient moins abondantes dans les bassins occupés par des juvéniles d'achigan à petite bouche, et plus abondantes dans ceux occupés par les adultes de cette espèce. La manipulation expérimentale des adultes appuyait l'hypothèse selon laquelle leur présence profite aux larves des autres espèces, mais le type de bassin influençait cette réponse. Les différences entre les effets des adults sur l'accumulation des larves dans les bassins du chenal principal par rapport aux bassins latéraux semblaient refléter l'influence de la dérive. Les avantages que la présence des adultes procuraient aux larves des autres espèces étaient probablement dus à leurs effets sur les juvéniles d'achigan et d'autres petits poissons, qui peuvent être les prédateurs les plus importants des larves de poissons. Un tel profil de co-occurrence entre les achigans adultes et les larves d'autres espèces à Baron Fork est déjà observé dans des lacs et des petits cours d'eau.

Received October 10, 1990
Accepted February 20, 1991
(JA749)

Reçu le 10 octobre 1990
Accepté le 20 février 1991

One historical dichotomy in ecology suggests that animal populations are predominately controlled by either abiotic or biotic factors. However, attempts to provide a broad "central theory" for ecology have recognized that abiotic and biotic factors often operate simultaneously (Menge and Sutherland 1987; Menge and Olson 1990). Schoener (1987) suggested that stream fishes are "intermediate to an unusual degree" in the extent to which abiotic or biotic factors predominate in the control of communities. This conclusion is supported by a large body of research. For example, Baltz et al. (1982) showed that competitive interactions between riffle sculpin (*Cottus gulosus*) and speckled dace (*Rhinichthys osculus*) in a California stream were dependent on water temperature. Schlosser and Ebel (1989) found that both flow regime and cyprinid predators significantly influenced invertebrates and fishes in a Minnesota headwater stream.

Stream fish larvae in particular are likely to be strongly influenced by both abiotic and biotic factors. Because of their relatively weak swimming ability, larval fish in streams may frequently be subject to drift (Gale and Mohr 1978; Muth and Schmulbach 1984; Brown and Armstrong 1985; Carter et al.1986; Corbett and Powles 1986). Harvey (1987) found that, although drift was negligible under nonflood conditions, virtually all floods in a small Oklahoma stream, Brier Creek, were fatal for larvae <10 mm total length (TL). The weak swimming ability of larvae may also lead to high risk of predation. Harvey (1991) showed that, between floods, predation on larval fish was important in Brier Creek. In addition, experiments indicated that survival of minnow (*Notropis* sp.) and sunfish (*Lepomis* sp.) larvae was higher in pools containing adult piscivores (largemouth bass (*Micropterus salmoides*)). In these pools, juvenile fishes (i.e. individuals 20–85 mm TL) were less abundant and largely confined to shallow water, apparently making them much less effective predators on larvae compared with juveniles in pools without adult piscivores.

Unpredictable floods and the restriction of large bass to certain pools in Brier Creek were both important to the survival of minnow and sunfish larvae. In larger streams, however, drift of larvae can be substantial during nonflood conditions, and movement of large piscivores is virtually unrestricted. In situations like these, do large piscivores still affect survival of

[1]Current address: Department of Zoology, Weber State University, Ogden, UT 84408-2505, USA.

larval fish? I addressed this question in a large Ozark upland stream by (1) measuring drift rates of larval fish, (2) censusing larvae and larger fishes, and (3) manipulating adult piscivores to measure their effect on the accumulation of larvae in pools.

Study Site

Baron Fork is a relatively swift, clear, fourth-order tributary of the Illinois River in northeastern Oklahoma, USA. Discharge ranged from 2.5 to 6.0 $m^3 \cdot s^{-1}$ in the study reaches between the towns of Eldon and Baron (35°57′N, 94°50′W upstream to 35°56′N, 94°36′W). Pools averaged 34 m^2 in area and 52 cm in depth. Riffles and runs were deep enough to allow all fishes access to virtually the entire stream. The most abundant fishes in the study area were central stoneroller (*Campostoma anomalum*), Ozark minnow (*Notropis nubilus*), cardinal shiner (*N. cardinalis*), longear sunfish (*Lepomis megalotis*), and smallmouth bass (*Micropterus dolomieui*). Moore and Paden (1950) provided more detailed information on the geology and fishes of the Illinois River drainage.

Materials and Methods

Drift

Drift was sampled at one site on Baron Fork from 12:00 on 22 May 1985 to 08:00 on 23 May 1985. I set four nets along a cross-stream transect for 1 h and repeated the sampling every 4 h. The nets had openings 30 × 45 cm, 363-μm-mesh fabric, and were anchored to the bottom with metal stakes (Wildlife Supply Company). Nets were positioned so that their long axes were horizontal and their tops extended above the water surface. Three of the nets sampled the entire water column, while one net sampled the upper 75% of the water column because depth at that location exceeded 30 cm. Water velocity through each net was measured with a propeller-type flowmeter (General Oceanics).

All drift samples were preserved in 10% formalin, and all larvae were counted from the four daytime and evening sampling times (12:00–20:00 and 08:00). I used a plankton splitter to fraction the nighttime samples (24:00 and 04:00) and counted the larvae in one-fourth aliquots. These subsamples contained up to 682 larvae.

Censuses

I conducted snorkeling censuses in Baron Fork to quantify patterns of co-occurrence among larger fishes and larvae. In May 1985 and May 1986, when cyprinid larvae were abundant, I recorded species (or family for larvae) and life history stage (adults, juveniles, larvae) for fishes present in pools. Fifty pools were censused each year; pools in particular were sampled because larvae that occupy the water column do not maintain position in substantial current. Although most larvae could be identified only to family, smallmouth bass larvae were readily distinguished.

Pools were defined as units with surface area of at least 1 m^2 and water column velocity <5 $cm \cdot s^{-1}$. After counting all fishes in the water column within a pool and estimating the pool boundary based on water velocity, I measured pool area and average water depth with a metre stick. In both years, estimates of pool boundaries based on water velocity were checked for the first five pools using a water velocity meter (Marsh-McBirney model 201). Pools within the main channel of the stream were distinguished from side pools. In some pools where larvae were very abundant and evenly distributed, the total number of larvae was estimated by extrapolating from a fraction of the total volume.

Because I hypothesized that both juvenile and adult smallmouth bass would affect the abundance of larvae of other species that occupied the water column, I examined these pool-specific census data using a four-way analysis of variance (ANOVA) with adult smallmouth bass presence/absence, juvenile smallmouth bass presence/absence, pool type (main channel, side), and year as factors. All possible interactions among these four factors were explicitly incorporated in the analysis. The response variable was the concentration of larvae in the water column (number per cubic metre, excluding smallmouth bass larvae). The importance of fishes other than smallmouth bass was examined in a second ANOVA which utilized the presence/absence of adult smallmouth bass, juvenile smallmouth bass, adult longear sunfish, juvenile longear sunfish, and adult *Notropis* as factors. Sunfish and *Notropis* were included in this analysis because they were abundant and are possible predators of minnow larvae. The response variable was again the concentration of larvae (other than smallmouth bass) in pools.

Experiment

To directly test the effect of adult smallmouth bass on abundance of minnow larvae, I manipulated adult bass abundance and measured the accumulation of larvae in four Baron Fork pools. Each pool received two trials of two different treatments: (1) no smallmouth bass or (2) one smallmouth bass 220–256 mm standard length (SL) tethered to an anchor by nylon line passing around the lower jar near its apex. Power and Matthews (1983) successfully used a similiar technique to restrict movement of adult largemouth bass. Length of the line was adjusted to allow the bass to range over the entire pool. Pool borders, defined by the 5 $cm \cdot s^{-1}$ water velocity contour, were marked with submerged surveyor's flags. I collected adult smallmouth bass for this experiment from Baron Fork by electrofishing.

Each trial began between 17:00 and 19:30 with an effort to remove all naturally occurring larvae from the water column of an experimental pool with a small seine and an aquarium net and then, in half the trials, addition of a tethered bass. I censused larval fish occupying the water column in the pool 22–26 h later. Because drift of larval fish into experimental pools was not controlled, the number of larvae present after each 22–26 h trial represented immigration minus losses from predation and emigration. Fishes other than adult smallmouth bass and larvae were not manipulated; all pools initially contained at least one juvenile smallmouth bass <80 mm TL and five juvenile longear sunfish. The experiment was conducted from 27 May to 1 June 1986, when cyprinids dominated the larval fish fauna in Baron Fork.

Because the accumulation of larvae was likely to depend in part on drift, I utilized two different pool types in the experiment: (1) side pools, which were characterized by little exchange of water with the main channel of the stream, and (2) pools within the main channel. The two side pools used in this experiment had average depths of 32 and 40 cm and areas of 9.6 and 10.2 m^2. The two main channel pools had average depths of 48 and 58 cm and areas of 4.9 and 5.0 m^2.

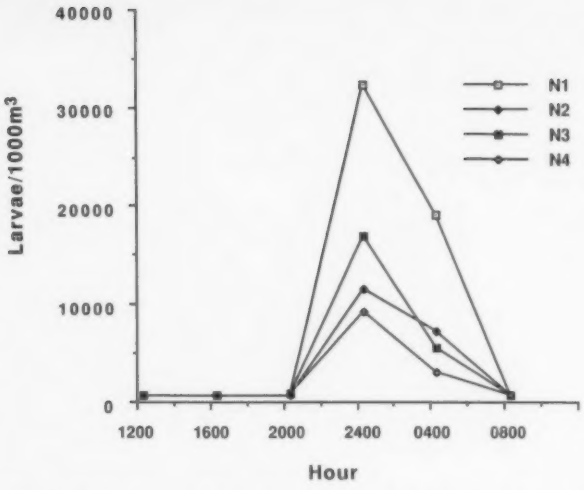


FIG. 1. Drift of larval fish in the Baron Fork of the Illinois River at Baron, Oklahoma, 22–23 May 1985. N1 – N4 represent nets at different locations along a cross-stream transect. N1: 1 m from the right bank (upstream perspective), water depth 18 cm; N2: 10 m from the right bank, depth 30 cm; N3: 6 m from left bank, depth 39 cm; N4: 2 m from left bank, depth 18 cm. The total stream width was 19 m.

The experimental design was thus partially hierarchal, in that there were two pools nested within each of two pool types (Winer 1971). I transformed larval abundance data $\ln(x + 1)$ prior to ANOVA to reduce significant variance heterogeneity in the raw data.

Results

Large numbers of larvae drifted at night (24:00 and 04:00); few were captured during the day (08:00, 12:00, and 16:00; Fig. 1). Because of the large difference between daytime and nighttime drift rates, Fig. 1 does not show that drift was slightly higher in evening samples (20:00) compared with daytime: the average concentration of larvae in the four nets was 11/1000 m^3 (SE = 0.9) for the 16:00 samples and 95 (SE = 8.7) for the 20:00 samples. Drifting larvae appeared to be concentrated along the stream margin: Net 1, 1 m from water's edge, had peak drift concentrations about two times higher than the highest concentration in any of the other three nets placed further from shore.

The census data indicated that both juvenile and adult smallmouth bass affected the concentration of larvae of other fishes in pools ($P < 0.01$ and $P < 0.02$, respectively). Pools containing juvenile bass had fewer larvae than pools without juvenile bass. Pools containing adult bass had higher concentrations of larvae than pools without adult bass (Fig. 2). There was no interaction between the juvenile and adult smallmouth bass effects. Pool type, year, and all the other interactions among the four main factors also did not significantly influence the concentration of larvae ($P > 0.15$). The second ANOVA, which included adult and juvenile sunfish and adult *Notropis* in addition to juvenile and adult smallmouth bass as factors, indicated that sunfish and *Notropis* did not significantly influence the concentration of larvae.

The accumulation of minnow larvae during experimental trials was substantial only in the two main channel pools when

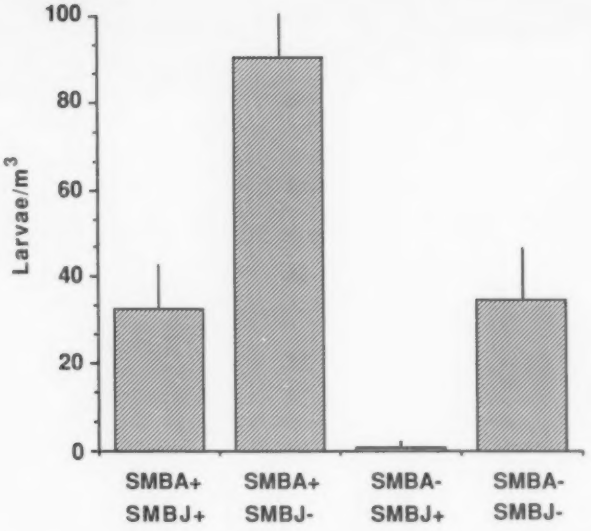


FIG. 2. Average concentrations of larvae in Baron Fork pools with different combinations of juvenile and adult smallmouth bass presence (+) / absence (−). The graph illustrates data from 50 pools in 1985 and 50 pools in 1986, including pools within the main channel and side pools. Vertical bars = 1 SE.

TABLE 1. Results of the adult smallmouth bass/larval fish experiment conducted in Baron Fork, Oklahoma, June 1986, showing the concentration (number/m^3) of minnow larvae that accumulated in pools during each of sixteen 22–26 h runs. The two replicates for each pool/bass treatment combination are separated by commas.

	Pool type			
	Main channel		Side pool	
Bass treatment	Pool 1	Pool 2	Pool 3	Pool 4
1 bass	107, 64	46, 33	10, 6	2, 0
0 bass	0, 4	0, 0	6, 7	1, 0

they contained adult bass (bass × pool type interaction, $P < 0.001$; Table 1). The effect of pool type probably reflects differences in drift input of larvae between main channel pools and side pools. Accumulation of larvae was also different between pools of the same type ($P < 0.005$), which may also be an indication of differences in drift input.

Discussion

This study suggests that both abiotic and biotic factors have important roles in the early life history of stream fish larvae occupying the water column of Baron Fork. The highest concentration of larvae drifting at night comprised 60% of the average concentration of larvae occupying pools during the day, which suggests a high nightly turnover rate of individuals in some locations. Even with this high rate of larval fish drift, effects of the presence of larger fish on the concentration of larvae were apparent: in natural pools, larvae were less abundant where juvenile piscivores were present and more abundant where adult piscivores were present. The experiment supported

the positive relationship between the abundance of larvae and the presence of adult bass indicated by the censuses.

While the censuses indicated that the positive effect of adult bass on larvae was independent of pool type, the experiment revealed a significant adult bass × pool type interaction. This conflict was apparently created by the experimental procedure. Because of the short-term nature of the experimental trials, the importance of differences in drift inputs to main channels versus side pools was magnified. The censuses, however, measured the result of drift and biotic processes on a longer time scale. The drift measurements, censuses, and the experiment taken together suggest that adult bass in side pools may have a positive effect on individual larvae for a longer period than they do in main channels. Adult bass in main channel pools appear to affect a larger number of larvae, but they may affect individual larvae for only short periods because of high larval drift rates.

The pattern of abundance for adult bass, juvenile fishes, and larvae evident in this study parallels results from lakes (Werner and Hall 1988) and small streams (Harvey 1991). Adult piscivores can affect juvenile fishes in a number of ways: by reducing the abundance of juveniles via predation, by causing habitat shifts (e.g. Fraser and Emmons 1984; Schlosser 1988; Harvey 1991), and by reducing the time that juveniles can allocate to feeding (Magurran et al. 1985; Godin 1986). All three of these mechanisms will benefit larval fish where juvenile fishes are significant predators of larvae.

The census data indicate that, while abundances of juvenile and adult smallmouth bass were negatively correlated ($r = -0.31$, $P < 0.01$, n (pools) = 83), the "protection" that adult piscivores provide the larvae of other species was not complete. There was no interaction between the effects of adult and juvenile smallmouth bass, meaning that juvenile bass had a negative effect on the concentration of larvae even when adult bass were present. The size and complexity of Baron Fork pools probably promote coexistence of adult and juvenile bass and allow juvenile bass some freedom from negative effects of larger piscivores. Also, because fish are not physically confined to individual pools in this stream (e.g. by shallow riffles), the composition of the fish assemblage in any one pool may change frequently.

The high rate of larval fish drift measured in this study raises questions about the costs and benefits of drifting for individuals. In contrast with the drift of larvae in a small stream during flood conditions (Harvey 1987), larvae survived drifting in Baron Fork during nonflood flow. Combined with the fact that predation risk for nocturnally drifting larvae is probably low, drifting itself may be no more risky for larval fish than staying in place. Thus, important costs and benefits would be linked to conditions in the habitats occupied by larvae before and after they drift. Relevant features of these habitats for larvae might include water velocity, food availability, and predation risk.

Physical conditions in side pools seem highly appropriate for larvae. Because of their minimal connections to the main channel and the predominance of microhabitats with zero water velocity, side pools offer larvae low risk of drift and require that larvae expend relatively little energy to maintain position. Differences in food availability among habitats may exist. Larvae occupying side pools may be able to feed on benthic invertebrates, while larvae occupying main channel pools cannot. By volume, the diets of minnow larvae collected from side pools in Baron Fork were dominated by chironomid larvae, while diets of minnow larvae collected from main channel pools were dominated by diatoms and rotifers (B. Harvey, unpubl. data). Warmer temperatures in side pools may also be favorable for larvae. While physical conditions and food availability may be best in side pools, predation risk appears to be strongly influenced by smallmouth bass regardless of pool type.

In addition to main channel pools and side pools, the edges of the main channel provide low-velocity habitat for larvae in large streams. Considering that larvae are known to drift close to shore (Brown and Armstrong 1985; this study), the edges of the main channel may provide only temporary residences for larvae. However, predation risk for larvae occupying shallow stream edges may be low because larger fish tend to avoid these areas (Power 1984; Harvey 1991).

Whether the initiation of drifting by larval fish in Baron Fork is a passive or active process remains unclear. This study suggests several ways that the ability to detect abiotic and biotic conditions in a given pool and to respond appropriately would be advantageous for larvae. Larvae might be less abundant in pools with juvenile bass, for example, because they respond to the presence or activity of juvenile bass by drifting. This mechanism may have contributed significantly to the experimental result that larvae accumulated where adult bass were present.

The survival of larval fish in Baron Fork appears to involve a dynamic interplay between abiotic and biotic factors. Large numbers of larvae occupying main channel pools and stream edge habitats probably drift nightly. Larvae in side pools may drift much less frequently, but whether individuals remain in side pools for extended periods is unknown. Predation risk for larvae varies in time and space depending on the presence or absence of at least two groups of larger fishes (juvenile and adult bass). The rate of larval drift, influenced by current, mediates the duration of periods of protection and risk that larvae experience from adult and juvenile bass, respectively.

Acknowledgements

L. Brown, S. Collins, A. Covich, B. Matthews, D. Perkins, M. Power, A. Stewart and S. Threlkeld made many valuable comments on earlier versions of the manuscript. B. Goldowitz provided aggressive editing of a recent version. J. J. Hoover loaned me essential equipment. M. Fleming provided assistance in the field. I received financial support from the University of Oklahoma Department of Zoology, the National Science Foundation (Dissertation Improvement Grant BSR 85-01200), the American Society of Ichthyologists & Herpetologists Raney Fund, and the University of Oklahoma Graduate Student Association.

References

BALTZ, D. M., P. B. MOYLE, AND N. J. KNIGHT. 1982. Competitive interactions between benthic stream fishes, riffle sculpin, *Cottus gulosus*, and speckled dace, *Rhinichthys osculus*. Can. J. Fish. Aquat. Sci. 39: 1502–1511.

BROWN, A. V., AND M. L. ARMSTRONG. 1985. Propensity to drift downstream among various species of fish. J. Freshwater Ecol. 3: 3–17.

CARTER, J. G., V. A. LAMARRA, AND R. J. RYEL. 1986. Drift of larval fishes in the upper Colorado River. J. Freshwater Ecol. 3: 567–577.

CORBETT, B. W., AND P. M. POWLES. 1986. Spawning and larva drift of sympatric walleyes and white suckers in an Ontario stream. Trans. Am. Fish. Soc. 115: 41–46.

FRASER, D. F., AND E. E. EMMONS. 1984. Behavioral responses of blacknose dace (*Rhinichthys atratulus*) to varying densities of predatory creek chub (*Semotilus atromaculatus*). Can. J. Fish. Aquat. Sci. 41: 364–370.

GALE, W. F., AND H. W. MOHR, JR. 1978. Larval fish drift in a large river with a comparison of methods. Trans. Am. Fish. Soc. 107: 46–55.

GODIN, J.-G. J. 1986. Risk of predation and foraging behaviour in shoaling banded killifish (*Fundulus diaphanus*). Can. J. Zool. 64: 1675–1678.

HARVEY, B. C. 1987. Susceptibility of young-of-the-year fishes to downstream displacement by flooding. Trans. Am. Fish. Soc. 116: 851–855.
1991. Larval fish survival in streams: the importance of biotic interactions. Oecologia (Berl.) (In press)
MAGURRAN, A. E., W. J. OULTON, AND T. J. PITCHER. 1985. Vigilant behaviour and shoal size in minnows. Z. Tierpsychol. 67: 167–178.
MENGE, B. A., AND A. M. OLSON. 1990. Role of scale and environmental factors in regulation of community structure. Trends Ecol. Evol. 5: 52–57.
MENGE, B. A., AND J. D. SUTHERLAND. 1987. Community regulation: variation in disturbance, competition and predation in relation to environmental stress and recruitment. Am. Nat. 30: 730–757.
MOORE, G. A., AND J. M. PADEN. 1950. The fishes of the Illinois River in Oklahoma and Arkansas. Am. Midl. Nat. 44: 76–95.
MUTH, R. T., AND J. C. SCHMULBACH. 1984. Downstream transport of fish larvae in a shallow prairie river. Trans. Am. Fish. Soc. 113: 224–230.
POWER, M. E. 1984. Depth distributions of armored catfish: predator-induced resource avoidance? Ecology 65: 523–528.
POWER, M. E., AND W. J. MATTHEWS. 1983. Algae-grazing minnows (*Campostoma anomalum*), piscivorous bass (*Micropterus* spp.) and the distribution of attached algae in a small prairie-margin stream. Oecologia (Berl.) 60: 328–332.
SCHLOSSER, I. J. 1988. Predation risk and habitat selection by two size classes of a stream cyprinid: experimental test of a hypothesis. Oikos 52: 36–40.
SCHLOSSER, I. J., AND K. K. EBEL. 1989. Effects of flow regime and cyprinid predation on a headwater stream. Ecol. Monogr. 59: 41–57.
SCHOENER, T. W. 1987. Axes of controversy in ecology, p. 8–16. *In* W. J. Matthews and D. C. Heins [ed.] Community and evolutionary ecology of North American stream fishes. University of Oklahoma Press, Norman, OK.
WERNER, E. E., AND D. J. HALL. 1988. Ontogenetic habitat shifts in bluegill: the foraging rate – predation risk trade-off. Ecology 69: 1352–1366.
WINER, B. J. 1971. Statistical principles in experimental design. McGraw-Hill, New York, NY. 907 p.

Trace Element Distributions in Aquatic Insects: Variations among Genera, Elements, and Lakes

Landis Hare, André Tessier, and Peter G. C. Campbell

I.N.R.S.-Eau, Université du Québec, C.P. 7500, Sainte-Foy (Québec) G1V 4C7, Canada

Hare, L., A. Tessier, and P. G. C. Campbell. 1991. Trace element distributions in aquatic insects: variations among genera, elements, and lakes. Can. J. Fish. Aquat. Sci. 48: 1481–1491.

The distribution patterns of trace element contaminants (As, Cd, Cu, Pb, Zn) among the tissues of freshwater insects (*Chironomus, Clinotanypus, Procladius, Hexagenia, Sialis*) are both taxon and element specific. In quantity terms (micrograms per animal), the gut is the major organ of Cd accumulation, while most of the As, Cu, Pb, and Zn accumulates in the body (i.e. animal minus gut and other organs). In concentration terms (micrograms per gram), Cd, Cu, and Zn are often highest in the gut, while Pb and As are not. Much of the As, and in some genera the Pb, appears to be bound externally. Respiratory and excretory structures generally contain small proportions of the total trace element burdens, except for Cu. Trace elements are not uniformly distributed along the gut but tend to accumulate either in the mesenteron (midgut) or in the proctodeum (hindgut), depending on the element and insect concerned. The distribution patterns of most of the trace elements vary little among populations of the mayfly *Hexagenia* from different lakes with the exception of Cd, for which the proportion of the total Cd burden localized in the gut increases markedly with increasing Cd concentrations in the whole nymph.

Les distributions inter-tissus des éléments traces (As, Cd, Cu, Pb, Zn) chez les insectes d'eau douce (*Chironomus, Clinotanypus, Procladius, Hexagenia, Sialis*) sont spécifiques au taxon ainsi qu'à l'élément trace. En termes de quantité (microgrammes par animal), l'intestin est l'organe majeur d'accumulation du Cd, alors que les éléments As, Cu, Pb et Zn sont accumulés en plus grande quantités dans le corps (c'est-à-dire l'animal moins l'intestin et d'autres organes). En termes de concentration (microgrammes par gramme), les éléments Cd, Cu et Zn sont normalement les éléments traces les plus abondants dans l'intestin, tandis que l'As et le Pb y sont peu élevés. La plus grande proportion de l'As, ainsi que le Pb chez certains genres, semble être liée à la surface extérieure de l'insecte. Les structures excrétrices et respiratoires contiennent généralement faibles proportions des quantités totales des éléments traces cités, à l'exception du Cu. Les éléments traces ne sont pas distribués de façon uniforme le long de l'intestin mais ont tendance à s'accumuler soit dans le mésentéron (partie mediane), soit dans le proctodéum (partie postérieure); la localisation précise varie selon l'élément et l'insecte étudiés. Les distributions des éléments traces chez *Hexagenia* varient peu entre les individus provenant de différents lacs pour tous les éléments traces, à l'exception du Cd pour lequel la proportion de métal localisé dans l'intestin croît avec une augmentation des concentrations de Cd dans la larve entière.

Received October 10, 1990
Accepted February 20, 1991
(JA752)

Reçu le 10 octobre 1990
Accepté le 20 février 1991

Animals in most freshwater systems are contaminated to some extent and thus can potentially be used as pollution biomonitors. Knowledge of the routes by which a species takes up contaminants is essential to its effective use as a biomonitor (NRCC 1988). Routes of contaminant uptake can be estimated by determining the distributions of contaminants within animals, e.g. the presence of a large proportion of a contaminant in the gills or the gut could suggest that it was taken up primarily from water or food, respectively (Luoma 1983; King and Davies 1987; Hare et al. 1991). The study of internal contaminant distributions can also be useful in identifying the tissues in which toxic effects are most likely to occur and in the planning of related histological and physiological studies. Within animals, contaminant concentrations can vary widely among respiratory, digestive, and muscle tissues of individual freshwater animals, including fish (e.g. Bendell-Young and Harvey 1989), molluscs (e.g. Tessier et al. 1984), and crayfish (e.g. Anderson and Brower 1978). Such patterns have been little studied in insects.

Freshwater insects have been little used as biomonitors, yet they are both common and are known to accumulate organic and inorganic pollutants (Ciborowski and Corkum 1988; Timmermans et al. 1989). The internal distributions of contaminants in insects have until recently been measured only in individuals exposed over short times to high concentrations of single pollutants in the laboratory (Sumi et al. 1984; Meyer et al. 1986; Seidman et al. 1986a, 1986b). Results of such studies are difficult to extrapolate to animals in nature, which often are subjected to long-term exposure to low concentrations of several contaminants, in both food and water. In addition, many of the microtechniques used to study internal contaminant distributions produce artifacts (i.e. many fixation and embedding procedures; Brunk and Sköld 1967; George et al. 1976) or cannot discriminate among contaminants and/or permit accurate measurement of their concentrations (e.g. using autoradiography, silver sulphide staining, and X-ray microprobe analysis). In contrast, the direct dissection of organisms allows the accurate quantification of individual contaminants in body parts, but

is limited by the extent to which organisms can be physically subdivided.

In the present study, aquatic insects from several taxonomic groups (Diptera, Ephemeroptera, Megaloptera) and having a variety of feeding habits (predators, detritivores, generalists) were dissected and the concentrations of several trace elements (As, Cd, Cu, Pb, Zn) were measured in various tissues. Comparisons were made among individuals collected from different lakes contaminated by trace elements.

Measurements of trace elements in shed nymphal skins (exuviae) and in adult insects were compared with those in whole nymphs to estimate the partitioning of trace elements between the surface and the interior of animals. Such information is used to assess the potential for trace element loss during nymphal moulting and the transfer of trace elements from aquatic to terrestrial systems through adult emergence. Animals used for this purpose had been exposed to trace elements in nature. In laboratory studies, animals are often exposed to high concentrations of dissolved trace metals in the absence of food over short time periods. Exposure by this latter means could result in a bias towards the surface binding of trace elements (e.g. Kormondy 1965; Frick and Herrmann 1990).

Study Areas

Insects were collected from 17 lakes located in southern Ontario and Quebec, Canada (Table 1). All of the lakes are contaminated to a greater or lesser degree by trace metals, either through direct input and fallout from nearby mines and smelters (Chibougamau, Rouyn-Noranda, Sudbury) or by long-range atmospheric fallout (Dorset, Eastern Townships, Quebec City). The ranges of total surficial sediment metal concentrations among these lakes are wide: Cd 0.3 – 12; Cu 2 – 2300, Pb 10 – 240, and Zn 40–400 $\mu g \cdot g$ dry weight^{-1}. All of the study lakes are located on Precambrian Shield bedrock with the exception of Lake Brompton which is located on sedimentary and volcanic rocks of Ordovician age in the Quebec Appalachians.

Methods

Sampling and Depuration

Multiple Ekman grab samples were collected in June (of several years; Table 1) at one shallow site (3–6 m) in each lake and sieved in the field using a 0.5-mm-mesh aperture net. Insects and sediment retained in the net were transferred to 4-L plastic bags with lake water and were transported to the laboratory in coolers maintained close to field temperatures. In the laboratory, insects were sorted from the remaining sediment. Nymphs of *Hexagenia* were dissected immediately, while the other taxa were left to depurate in lake water for 2 d, in the dark, at field temperatures. The water was changed twice daily to minimize coprophagy.

Five insect taxa were chosen for study: the mayfly *Hexagenia limbata* (Serville) (Ephemeroptera), the alderfly *Sialis* sp. (Megaloptera), and the midges (Diptera, Chironomidae) *Chironomus* sp. (Chironominae), *Clinotanypus* sp. (Tanypodinae), and *Procladius* sp. (Tanypodinae). *Sialis* and the chironomid genera were not identified to species. Nymphs/larvae of each genus were dissected from two moderately to highly contaminated lakes located in the mining areas of either Sudbury and/or Rouyn-Noranda. Lake pairs were chosen according to the abundance of each genus in the lakes sampled. Insects from contaminated lakes were used so as to minimize problems of trace element detection in the body parts of these small animals. In order to study the influence of ambient contaminant concentrations on the body part distribution of trace elements in more detail, *H. limbata* nymphs were collected from several additional lakes (Table 1) showing a wide range of sediment trace element concentrations.

To quantify the proportion of trace elements bound externally on nymphs, nymphal exuviae of recently emerged (<12 h) *H. limbata* adults were collected on the surface of Lake St. Joseph at the same time as nymphs were collected from this lake. In addition, adults of *H. limbata* (hereafter referred to as *Hexagenia*) were reared from Lake Joannès nymphs that had been held in the laboratory in sediments collected from that lake.

Dissection

Individuals were dissected with stainless steel instruments in small amounts (2 mL) of deionized water under a microscope at magnifications of 120 and 250×. As each part of an animal was removed, it was placed on a preweighed piece of acid-washed Teflon which was held in a longitudinally cut piece of Tygon or Teflon tubing cemented or sewn onto a plastic petri dish (Hare et al. 1989). The parts of several animals were pooled (Table 1) in order to obtain sufficient quantities of tissue for weighing and analysis.

Hexagenia and depurated *Sialis* nymphs were dissected in the following manner. An animal was immobilized by a ventral incision between the head and thorax (which severed the gut and nerve cord) and the abdominal gills were removed. A mid-ventral incision was made along several posterior abdominal segments to extract the gut from the posterior end of the animal. The Malpighian tubules were separated from the gut and, in the case of the nondepurated *Hexagenia*, the gut was opened to remove its contents (Hare et al. 1989). The gut was cut into three portions: the anterior and posterior halves of the mesenteron (midgut) and the proctodeum (hindgut).

In the case of the three chironomid genera, the head and the terminal portion of the last abdominal segment were cut off to allow the withdrawal of the gut from the body. There was little fluid loss, since the elasticity of the body wall sealed the body cavity after withdrawal of the gut. The gut was separated into four regions: the esophagus (or stomodeum), the anterior dilated portion of the mesenteron, the posterior mesenteron, and the proctodeum (Fig. 1). The Malpighian tubules remained attached to the proctodeum.

Analytical Procedures

To minimize trace element contamination, all labware was soaked in 15% nitric acid for 24 h and rinsed repeatedly in deionized water prior to use. Deionized water for all purposes was obtained from a Milli-Q3RO/Milli-Q2 system (Millipore Corp.). Manipulations of samples were performed when required under a filtered air hood.

The petri dish containing the animal parts was placed in a freezer at −40°C for at least 1 h and then in a lyophiliser to dry the tissues for at least 12 h. Each pooled animal part was weighed on its piece of Teflon with a Mettler ME30 electronic microbalance (balance pan covered with Teflon). Digestion procedures varied somewhat among samples, a consequence both of the refinement of methods with time and the competing needs of parallel studies. Dried insects were digested either in

TABLE 1. Locations of the study lakes, times of sampling (June of each year), and the number of individuals of each genus dissected from each lake.

Lake	Genus (no. of samples × no. of individuals)	Year
Sudbury, Ontario		
Clearwater (46°22′N, 81°03′W)	*Procladius* (1 × 5)	1988
	Sialis (2 × 4)	1988
Fairbank (46°28′N, 81°25′W)	*Hexagenia* (1 × 5)	1988
McFarlane (46°25′N, 80°57′W)	*Chironomus* (1 × 6)	1988
Wavy (46°17′N, 81°06′W)	*Procladius* (1 × 7)	1988
Dorset, Ontario		
Bigwind (45°03′N, 79°03′W)	*Hexagenia* (3 × 5)	1988
Gullfeather (45°06′N, 79°01′W)	*Hexagenia* (1 × 2)	1988
Rouyn-Noranda, Quebec		
Bousquet (48°14′N, 78°34′W)	*Clinotanypus* (1 × 14)	1988
	Hexagenia (3 × 5)	1988
La Bruère (48°09′N, 78°56′W)	*Hexagenia* (3 × 5)	1988
Caron (47°56′N, 78°58′W)	*Chironomus* (3 × 5)	1988
	Hexagenia (3 × 5)	1988
D'Alembert (48°23′N, 79°01′W)	*Hexagenia* (3 × 5)	1988
	Sialis (3 × 8)	1990
	Procladius (2 × 14)	1990
Heva (48°11′N, 78°19′W)	*Clinotanypus* (1 × 8)	1989
	Hexagenia (1 × 8)	1989
Joannès (48°11′N, 78°41′W)	*Hexagenia* (3 × 5)	1987
Opasatica (48°06′N, 79°17′W)	*Hexagenia* (3 × 5)	1988
Chibougamua, Quebec		
aux Dorés (49°54′N, 74°18′W)	*Hexagenia* (1 × 5)	1987
Norhart (49°29′N, 74°26′W)	*Hexagenia* (3 × 5)	1987
Eastern Townships, Quebec		
Brompton (45°25′N, 72°09′W)	*Hexagenia* (3 × 5)	1987
Quebec City, Quebec		
St. Joseph (46°55′N, 71°40′W)	*Hexagenia* (4 × 10)	1989
Tantaré (47°04′N, 71°32′W)	*Hexagenia* (1 × 4)	1987

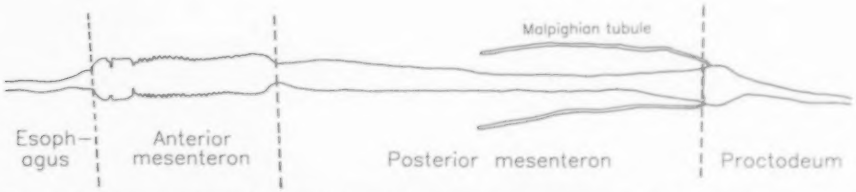


FIG. 1. Gut of a generalized chironomid larva indicating the four regions in which trace element measurements were made. Two of the four Malpighian tubules are shown.

thickwalled, screw-cap, Teflon vials (animals from Lakes Joannès and St. Joseph) or in Teflon bombs (other lakes) in hot concentrated nitric acid (Aristar grade; 100 μL·mg tissue dry weight^{-1}). Digestion was carried out either in a water bath at 70°C for 48 h (Lake Joannès), a pressure cooker at 120°C for 4 h (Lake St. Joseph), or in a microwave oven up to a pressure of 2760 kPa for ≈1 min (other lakes).

Cooled digested samples were diluted with deionized water and trace element concentrations were measured either by flameless atomic absorption spectrophotometry (Varian GTA-95 graphite tube atomizer; As, Cd, Cu, Pb) or flame atomic absorption spectrophotometry (Varian AA-575; Zn). Repeated measures of similar-sized samples of a certified reference material (lobster hepatopancreas, Tort 1, National Research Council of Canada, Ottawa, Ont.) varied little over time (coefficient of variation 3–7%; $n = 10$ for each element) and were close to the expected certified mean values (within 3.5–6.0%; $n = 10$ for each element).

Results and Discussion

General Trends

In all of the genera studied, most of the mass was represented by the body (tissues remaining after dissection) (Fig. 2). Similarly, the majority of the Zn present was located in the body portion (Fig. 2), indicating that concentrations of this element generally do not differ greatly among the various parts. However, substantial quantities of Zn were also present in the guts of two genera, *Hexagenia* and *Sialis* (Fig. 2), which reflects the somewhat higher concentrations of Zn in their guts

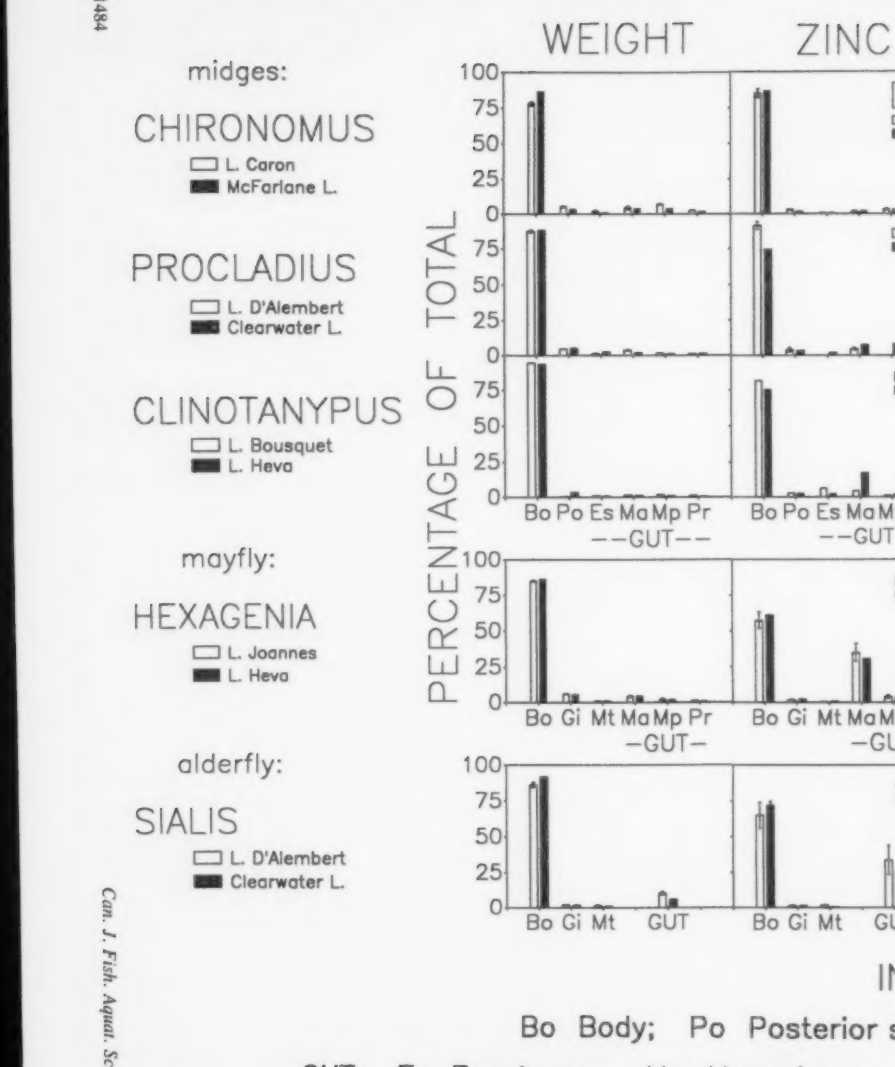
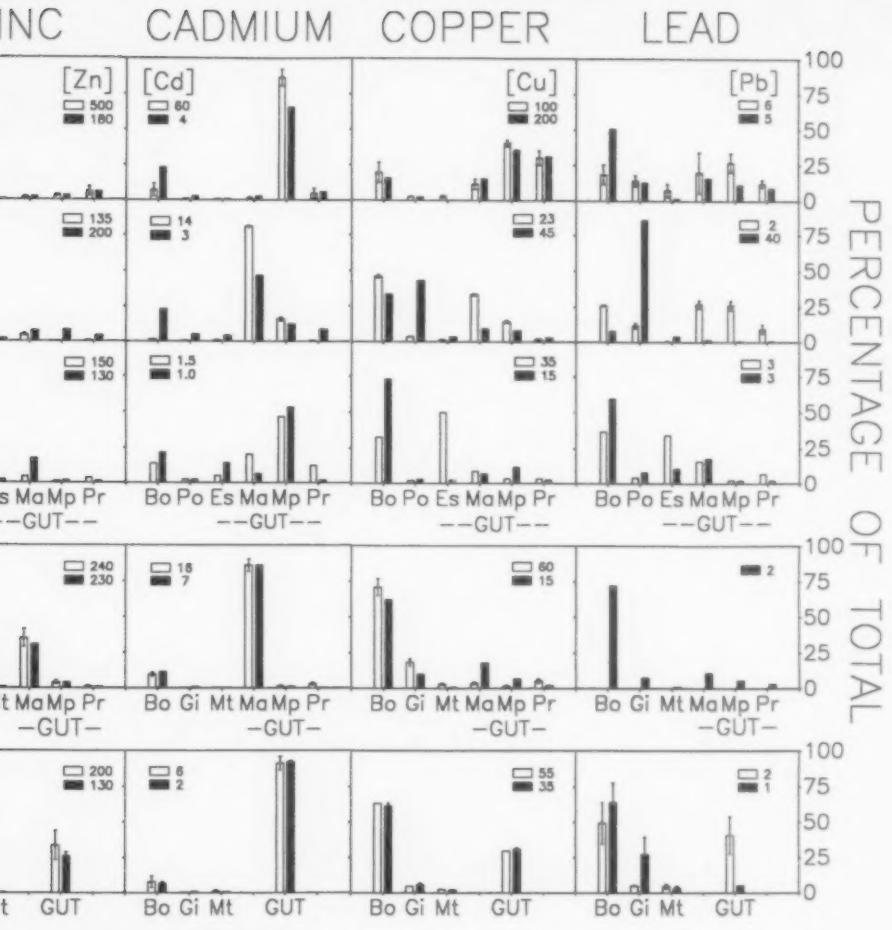


FIG. 2. Percentages of whole-animal dry weight and trace element burdens in the various p
genus from a given lake are available, mean values with their standard deviations are indica
trace element concentrations ($\mu g \cdot g^{-1}$) for whole animals from each lake. No data for Pb



INSECT PARTS:

rior segment; Gi Gills; Mt Malpighian tubules

on – anterior; Mp Mesenteron – posterior; Pr Proctodeum

arious parts of five aquatic insect genera, each collected from two lakes. Where multiple samples for a given e indicated. The number of samples per genus per lake is given in Table 1. Values given in the panels are for Pb are available from Lake Joannès.

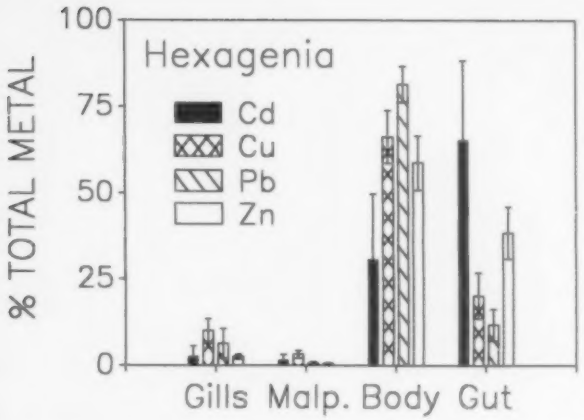


FIG. 3. Mean percentages (±SD, $n = 12$) of whole-animal metal burdens represented by each of the body parts of *Hexagenia* nymphs collected from lakes listed in Table 1 (Malp. = Malpighian tubules).

compared with their other parts. Arsenic (data not shown) was localized to an even greater extent in the body portion of the single genus studied, i.e. the proportions of As in the parts of *Hexagenia* were body 95±4%, gills 2±2%, and gut 3±2% ($\bar{x}$ ± SD, $n = 7$ from Lake Joannès). In marked contrast with Zn and As, the bulk of the Cd in all genera was localized in the gut (Fig. 2), where Cd concentrations often exceeded those in other parts by several orders of magnitude.

Copper tended to be localized in the body portion except in *Chironomus* in which greater quantities were present in the gut. Lead also tended to be associated with the body although the distribution patterns are much more variable among genera and between lakes. For example, in replicate samples of *Sialis* from each of two lakes, either 5 or 45% of the Pb was located in the gut (Fig. 2). Similarly, the proportions of Cu and Pb measured in the esophagus of *Clinotanypus* were very different between the two lakes studied; however, the higher values (Fig. 2, Lake Bousquet) may represent an artifact, as these measurements are based on a single pooled sample and are the only case in which large quantities of metals were measured in the esophagus of any genus.

A striking difference between lakes was also observed in the quantities of Cu and Pb located in the posteriormost abdominal segment (Po) of *Procladius* (Fig. 2). In this case, however, the higher unreplicated values cannot be dismissed, since in a third lake even higher proportions were measured in the posteriormost segment of this genus (Wavy Lake, data not shown; 80% of Cu and 95% of Pb in posteriormost segment). Possible explanations for this difference are either that the species of *Procladius* may be different in the two lakes or that the proportions of Cu and Pb accumulated in the posteriormost segment increase with increasing organism trace metal concentrations (Fig. 2; Wavy Lake whole larvae contained 85 μg Cu·g^{-1} and 35 μg Pb·g^{-1}). This latter possibility should be tested on larvae of a wide range of metal concentrations.

Constancy of Patterns among Lakes

For a given trace element the distribution pattern within each genus was on the whole similar between the two lakes studied, in spite of differences in trace element concentrations between individuals from the lakes (Fig. 2). This suggests that the distribution patterns observed may be independent of trace element concentrations in the whole insect.

This hypothesis was tested on a larger data set comprising nymphs of the mayfly *Hexagenia* collected from many lakes having a wide range in sediment trace element concentrations. Overall, the metal distribution patterns observed for nymphs from the two lakes studied initially (Fig. 2) resembled those for the larger data set (Fig. 3), i.e. the bulk of the Cu, Pb, and Zn was located in the body, while the bulk of the Cd was located in the gut. However, a closer examination of the data for Cd suggests that there was substantial variability in the distribution pattern for Cd among nymphs from different lakes, as evidenced by the large standard deviations around the means for this metal (Fig. 3).

The proportion of a trace metal located in that metal's major organ of accumulation was compared with the concentration of the metal in whole nymphs (Fig. 4). The proportion of Cd contained in the gut was positively correlated with the log of whole-animal Cd concentrations (Fig. 4; Pearson product-moment correlation coefficient (r) = 0.75, $0.002 > P > 0.001$). Since animal Cd concentrations tend to be a function of environmental Cd concentrations (Hare et al., in prep.), these results suggest that given higher Cd concentrations in the environment both the quantity and proportion of Cd stored in the gut will increase.

In contrast with Cd, the proportion of Zn in the body shows a significant negative correlation with the log of whole-animal Zn concentrations (Fig. 4; $r = 0.62$, $0.02 > P > 0.01$). This suggests that nymphs contaminated to a greater extent than those measured in the present study could contain the bulk of their Zn in the gut. Comparable measures for Pb were significantly positively correlated (Fig. 4; $r = 0.79$, $0.02 > P > 0.01$); however, the calculated value of the intercept on the vertical axis (65%) suggests that even at low Pb concentrations the bulk of this metal would be found in the body portion. No significant correlation between comparable Cu values was observed (Fig. 4; $r = 0.35$, $P > 0.2$) and thus the bulk of the Cu should always lie in the body portion of nymphs.

Since trace element concentrations in aquatic insects can be correlated with nymph size (Smock 1983; Darlington et al. 1987), the relationships above (Fig. 4), although based on differences among nymphs from different populations, could also apply to the members of a single population. That is, the distribution pattern of a trace element within individuals from the same lake may vary according to their size and age. This possibility remains to be tested.

The ranges in concentration of metals in whole *Hexagenia* nymphs from the various lakes differed greatly among metals and increased in the following order: Zn 2.0×, Pb 3.5×, Cu 5.0×, and Cd 125× (Fig. 4, note log scale for [Cd]). The ranges of corresponding concentrations of total metal in surficial sediment were greater for all metals except Cd but increased in the same order: Zn 10×, Pb 15×, Cu 20×, and Cd 30× (data not shown). The wide range of Cd concentrations in organisms compared with those in sediments suggests that Cd is stored in nymphs to a greater extent than are the other metals. Furthermore, the similarity in the order of the ranges for metals in organisms and in sediments suggests that organism metal concentrations are a function of environmental metal concentrations.

Internal versus External Localization of Trace Elements

The trace elements measured in aquatic insects can be localized both externally on the chitinous body covering and inter-

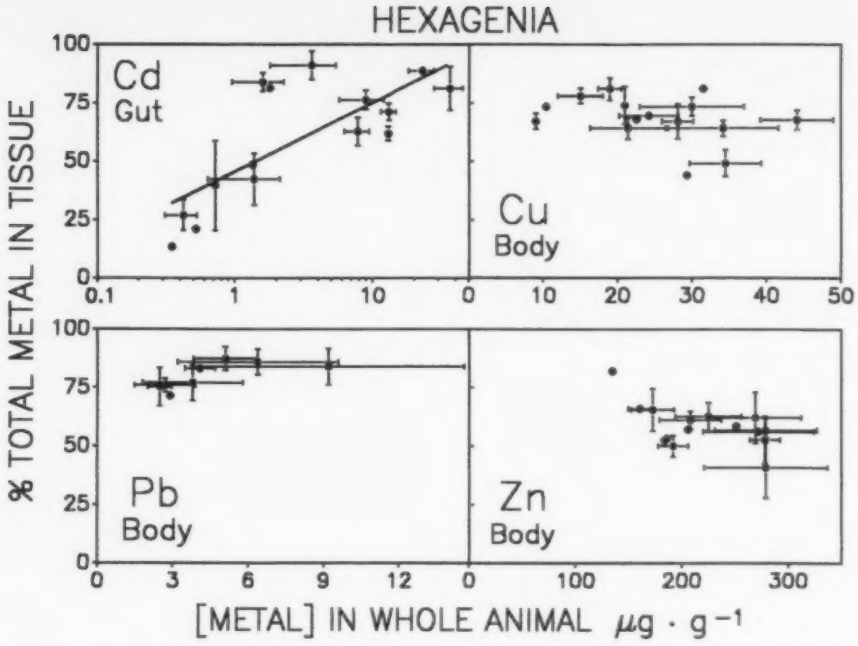


FIG. 4. Comparisons between the mean (± SD) percentage of metal found in the major storage tissue for each metal, with the mean (± SD) metal concentrations in whole *Hexagenia* nymphs collected from various lakes (Table 1). Log-linear regression of Cd: $r^2 = 0.56$. Note the logarithmic scale for [Cd].

nally in body tissues. In the mayfly *Hexagenia*, trace element concentrations in exuvial parts were equal to or greater than those in corresponding nymphal parts (Fig. 5). Metal concentrations were highest in the chitinous portion of the gut lining shed with the exuvium; however, given its small weight, it represented only a minor proportion of the total exuvial metal content (Fig. 5). Likewise, given the small proportion of the whole-gut weight represented in the exuvium (1%), trace elements associated with the chitinous gut lining represented small proportions of the whole gut burden: Cd 10%, Cu 5%, and Zn 2%.

The body portions of nymphs and exuviae always represented the bulk of the trace metal content in spite of their low metal concentrations (Fig. 5). The weight of the exuvium body represents ≈10% of that of the whole body and thus the proportions of each metal associated with the nymph body covering were approximately Cd 30%, Cu 15%, and Zn 5%. The exuvial gills, given their high surface area to volume ratio, represent a large proportion, ≈30%, of the weight of the gills of the whole nymph, and correspondingly high proportions of trace metals were associated with the shed exuvial gills: Cd 70%, Cu 30%, and Zn 40%. Based on the above values, the proportions of trace elements in the whole nymph associated with the entire animal surface were estimated at approximately Cd 40%, Cu 20%, and Zn 10%.

Comparisons of trace element concentrations were also made between recently emerged *Hexagenia* adults and their nymphal exuviae. It should be noted that adult/exuvium comparisons may be biased by metal losses during and after moulting, e.g. losses of Cd through postmoulting defecation by the adults of some terrestrial insects can represent 50% of the larval Cd burden whereas losses of Cu or Zn are apparently negligible (Aoki and Suzuki 1984).

Final instar exuviae and emergent adults had comparable concentrations of Cd, Cu, and Zn (Fig. 6); however, the exuvium, given its small weight (≈25% of adult weight), represented minor proportions of whole-nymph trace element burdens. Arsenic was present in the exuvium but was not detectable in adults (Fig. 6) and thus a high proportion of the As associated with *Hexagenia* nymphs appears to be bound on/in the exoskeleton. A similar pattern has been observed for As in several stream-dwelling insects (Cain and Luoma 1990). Aluminum also appears to be largely associated with the surfaces of aquatic insects (Frick and Herrmann 1990).

Much of the Pb associated with aquatic insects from several taxonomic groups appears to be bound externally, e.g. Ephemeroptera (*Hexagenia*; Hare et al. 1991), Diptera (*Chironomus*; Krantzberg and Stokes 1988), and Odonata (*Libellula* and *Aeshna*: Meyer et al. 1986). In the present study, the positive correlation observed between the proportion of Pb associated with the body of *Hexagenia* and whole-nymph Pb concentrations (Fig. 4) is consistent with increasing quantities of Pb bound to the surface of organisms living along a gradient of increasing environmental Pb concentrations.

Both the nymph/exuvium and the adult/exuvium comparisons were consistent in suggesting that approximately 20–25% of the Cu and 10% of the Zn associated with nymphs of *Hexagenia* was bound to the exoskeleton. There was, however, a substantial difference between the estimated values for Cd; nymph/exuvium and adult/exuvium comparisons suggest that either ≈40 or ≈7%, respectively, of the whole-animal Cd burden was externally bound. This difference was consistent with, and can be explained by, the previously observed positive relationship between Cd concentrations in the nymph and the pro-

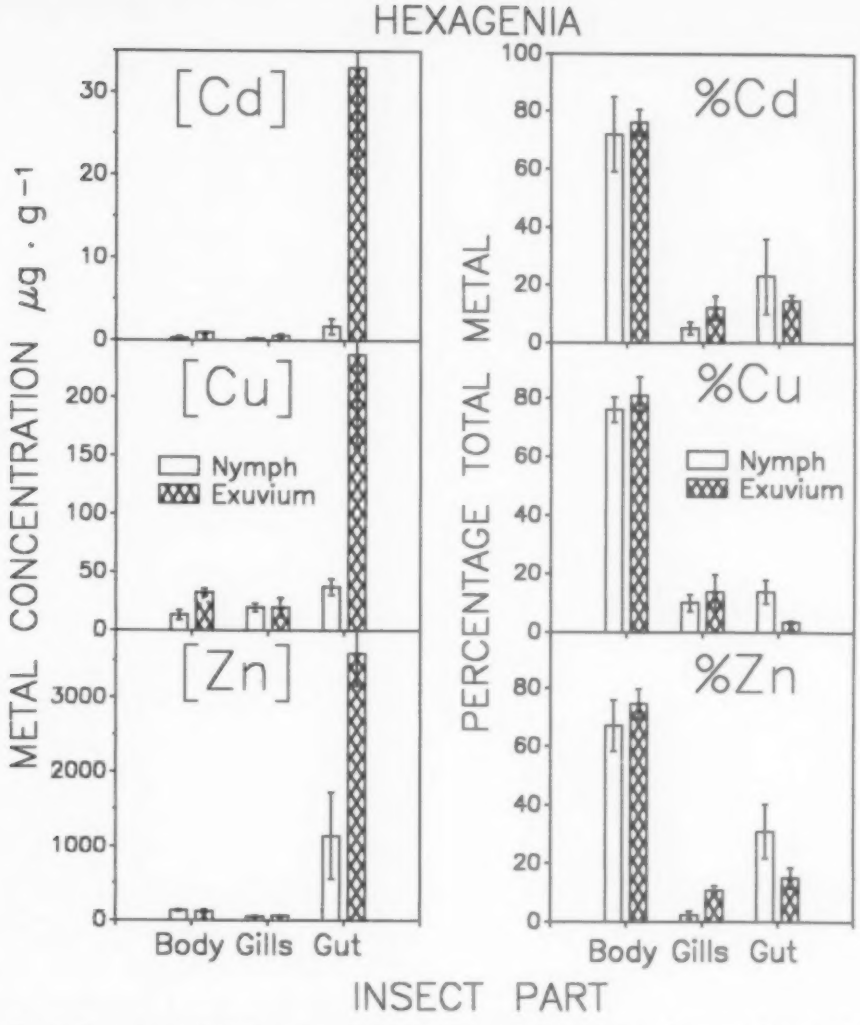


FIG. 5. Comparisons of both the concentrations and the proportional distributions of trace metals among the body parts of final instar nymphs and final instar exuviae of *Hexagenia* collected in Lake St. Joseph, Quebec.

portion of Cd that was associated with the gut (i.e. is internal; Fig. 4). Nymphs on which the adult/exuvium comparisons were made (from Lake Joannès) had much higher Cd concentrations (50×) and a higher proportion of Cd localized in the gut (80%) than did nymphs on which the nymph/exuvium comparisons were based (from Lake St. Joseph; 30% of Cd in the gut).

In addition to the possible influence of trace element concentrations in nymphs, environmental variables such as ambient pH will also be important in determining the degree of surface binding of some trace metals (Krantzberg and Stokes 1988). Furthermore, the proportion of trace elements bound externally will tend to vary negatively with body size, since the ratio of the surface area of an animal to its volume decreases with increasing body size. Such a tendency will be reinforced if there is an increase over time in the quantities of trace elements stored internally, e.g. in granules. Nymphs used in the above comparisons were in or near the final instar and thus the estimated proportions of externally bound metal should represent minima. The proportion of trace elements bound externally can also vary according to the age of the exoskeleton (Hare et al. 1991), i.e. for a given instar, recently moulted individuals should have lower concentrations of trace elements bound externally than those about to moult.

Trace elements associated with the chitinous exoskeleton are unlikely to have toxic effects on the insect, but could be taken up by predators that consume these insects whole. Trace elements on the exoskeleton will remain in the aquatic system (the exoskeleton is shed periodically), while those absorbed internally can be transferred to the terrestrial system, on emergence of the adult insect, to be consumed there by terrestrial predators such as birds (Nyholm 1981).

Gut

Although concentrations of Zn, Cu, and Pb were often highest in the gut, the bulk of these metals was generally found in the body portion (Fig. 2). A similar pattern has been observed

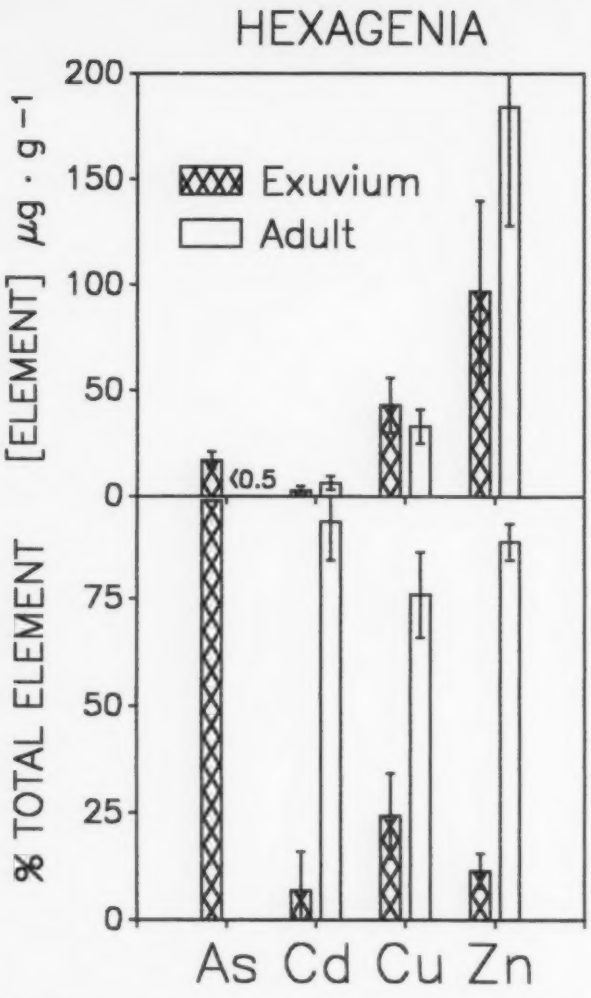


FIG. 6. Comparisons of both the concentrations and the proportional distributions of trace elements among the body parts of *Hexagenia* adults (subimago stage) and their final instar exuviae. Adults were reared in the laboratory from nymphs collected in Lake Joannès, Quebec.

for Pb in dragonflies (Odonata; Meyer et al. 1986). In contrast, Cd is largely associated with the insect gut in both aquatic (Seidman et al. 1986a; Hare et al. 1991; this study) and terrestrial (Aoki et al. 1984; Suzuki et al. 1984) taxa. The potentially large quantities of trace metals present in the gut could be stored in granules and/or lysosomes which have been observed in both aquatic (Seidman et al. 1986b) and terrestrial (Jeantet et al. 1977; Tapp and Hockaday 1977) insects. The rate at which such storage structures are excreted could determine the capacity of a given species to resist the toxic effects of metals (Humbert 1977). The depuration of metals from the gut could also be favored by their binding to and excretion with the peritrophic membrane, a protective chitinous sheet that is produced continuously by the mesenteron and excreted from the anus at rates of up to several millimetres per hour (Waterhouse 1954).

The digestive tract and accessory organs (the hepatopancreas, midgut gland, or digestive glands) are the major storage sites for Cd, Cu, and Zn in both decapod crustaceans and in marine deposit-feeding molluscs, e.g. Zn and Cu (Bryan 1968), Cd and Zn (Coughtrey and Martin 1976), Cd and Zn (Bryan and Hummerstone 1978), Cd (Ray et al. 1980), Zn (White and Rainbow 1984), Cd (Engel et al. 1985), Cd (Uthe and Chou 1987), and Cu (Bagatto and Alikhan 1987). The functions of these accessory organs are no doubt carried out by the gut in insects, suggesting that there is some similarity in the patterns of metal storage among these disparate groups of invertebrates. In contrast, burdens and concentrations of these trace metals in some suspension-feeding freshwater molluscs are much higher in the gills and mantle than in the digestive gland (Tessier et al. 1984).

The gut of aquatic insects can be subdivided into regions based on differences in gross anatomy (Fig. 1), the presence or absence of a cuticular lining (Chapman 1984), and the proportions of various cell types present (Pierson 1956). These structural differences imply corresponding functional differences that could lead to differences in trace metal accumulation along the gut. In addition, the concentrations of trace elements available for uptake from gut contents will also vary among gut regions depending on the conditions in the gut lumen. The presence and type of digestive enzymes (Terra 1990) and the pH (Phillips et al. 1986) have all been shown to vary along the length of the insect gut.

In the genera studied herein, the cuticle-lined foregut (or stomodeum) consists simply of an esophagus (crop and gizzard absent) and thus probably functions only in the transport of food from the mouth to the midgut and not in its digestion or absorption. Low concentrations of trace elements were usually measured in this region (Fig. 2 and 7).

The midgut, or mesenteron, functions in the production of digestive enzymes and in nutrient absorption, while the chitin-lined hindgut, or proctodeum, is implicated in the reabsorption of salts, water, and other substances from the urine and faeces and in defecation (Chapman 1984; Dow 1986). In the aquatic genera studied herein the region of greatest metal concentration varied according to the genus and metal under consideration (Fig. 2 and 7). Concentrations of Cd and Zn were generally highest in the mesenteron region with the exception of *Chironomus*, in which concentrations of Zn were highest in the proctodeum (Fig. 7). Copper concentrations were highest in the proctodeum or, in the case of *Procladius*, in the mesenteron. Pb concentrations tended to be similar among gut regions (Fig. 7). In the gut tissues of terrestrial insects, trace metals tend to be concentrated in the mesenteron, where they are stored either in the form of granules (Jeantet et al. 1977; Humbert 1978) or in cytolysosomes (Tapp and Hockaday 1977).

Even within a gut region, trace element concentrations differed substantially. For example, in members of the family Chironomidae, Cd was found largely in the anterior region of the mesenteron in *Procladius* (and in the mayfly *Hexagenia*) but in the posterior region of the mesenteron in *Clinotanypus* and *Chironomus* (Fig. 2 and 7), possibly in membrane-enclosed crystals (Seidman et al. 1986a, 1986b). These patterns do not correspond to differences in feeding habits among the genera; *Chironomus* is a deposit/suspension feeder (Johnson 1987), while *Clinotanypus* and *Procladius* tend to have more predatory feeding habits (Roback 1976 and Sephton 1987, respectively). Thus they are probably a consequence of differences in the functional and/or structural organization of the mesenteron among these genera. A gradient of functions along the mesenteron has been reported previously for both chironomid (Pier-

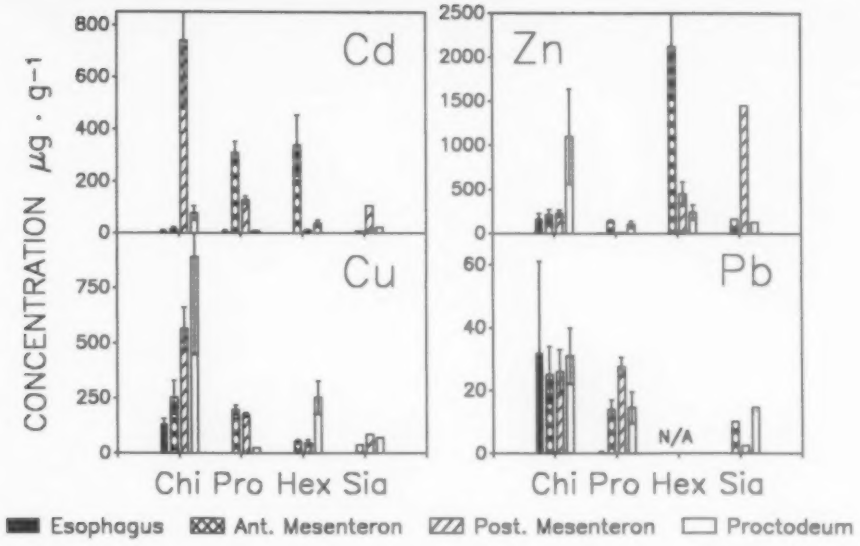


FIG. 7. Variations in trace metal concentrations along the guts of four insect genera. Values are means (± SD), with the exception of those for *Sialis* (a single pooled sample). Organisms were collected from either Lake Caron (Chi = *Chironomus*), Lake D'Alembert (Pro = *Procladius* and Sia = *Sialis*), or Lake Joannès (Hex = *Hexagenia*). N/A = measurements not available.

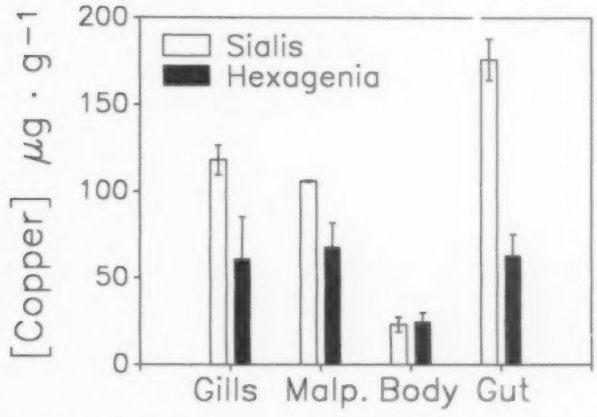


FIG. 8. Comparisons of mean (± SD) Cu concentrations among the body parts of *Sialis* and *Hexagenia* collected fom Clearwater Lake or Lake D'Alembert, respectively (Malp. = Malpighian tubules).

son 1956) and mosquito larvae (Clements 1963). These differences suggest that generalizations about internal trace metal distributions based on taxonomic or nutritional similarities among insects should be made with caution.

Respiratory and Regulatory Organs

Trace elements were measured in respiratory (gills) and excretory structures (Malpighian tubules) of *Hexagenia* and *Sialis*. These structures never contain large quantities of any trace element compared with the quantities present in the body (Cu, Pb, Zn) or in the gut (Cd) (Fig. 2). Of the elements studied, Cu is distinctive in being present in fairly high concentrations in the gills and Malpighian tubules (Fig. 8) and in higher concentrations in the proctodeum than in other gut regions (of *Hexagenia* at least; Fig. 7). A tentative explanation for this pattern could be the following.

Copper-based blood pigments are not present in insects. Copper extracted from body fluids by the Malpighian tubules could be in part stored in granules (Sohal et al. 1976) and in part excreted into the gut at the juncture of the mesenteron and the proctodeum (Fig. 1). Copper-containing granules have been observed in the Malpighian tubules of Trichoptera (Darlington and Gower 1990). In the proctodeum, Cu could be reabsorbed, perhaps by cells resembling the so-called chloride cells (Komnick 1977; Chapman 1984), and stored in granules (Ballan-Dufrançais 1974). The high proportions of Cu measured in the gills suggest that the initial source of Cu to the body fluids may be from water via the gills.

Copper and Pb distributions in *Procladius* from two Sudbury area lakes were unique in that both the quantities and concentrations of these metals were higher in the terminal abdominal segment than in any other animal part (Clearwater Lake, Fig. 2; Wavy Lake, data not shown). Possible sites of trace metal accumulation in this segment could be either the claws of the posterior prolegs or the anal tubuli. The anal tubuli are thought to function in ionic regulation, at least in mosquito larvae (Stobbart and Shaw 1974), and thus could also play a role in the storage and exchange of metals such as Cu and Pb. Trace metals have been detected previously in the anal tubuli of *Chironomus* (Krantzberg and Stokes 1990). Why this pattern should be observed for only one of the three chironomid genera studied bears further examination.

Conclusions

The study of contaminant distributions within aquatic insects is a useful extension of whole-animal studies, since, for a minimum of extra effort and expense, information can be obtained on the potential sites and mechanisms of contaminant exchange and toxicity within these animals. In addition, potential routes

of contaminant uptake can be determined, knowledge of which will facilitate the use of these animals as biomonitors of contamination. Such information is also useful in the design of complementary histological and biochemical studies aimed at characterizing processes at the tissue and cell levels. Measurements of the internal versus external localization of trace elements can be used to quantify moult-related losses of elements during insect development and the transfer of trace elements from the aquatic to the terrestrial system.

The results of the present study suggest that for a given insect taxon the internal distribution pattern of each trace element is fairly distinctive. Among taxa, the distribution patterns of both Cd, which is largely localized in the gut, and Zn, which is found in the body, are fairly constant, while those of Cu and Pb are more variable among both taxa and lakes.

Acknowledgements

The authors acknowledge funding from the Natural Sciences and Engineering Research Council of Canada and the Fonds pour la Formation de Chercheurs et l'Aide à la Recherche du Québec. Technical and field assistance was provided by R. Rodrigue, G. Tardif, and B. Veilleux. Valuable comments on the manuscript were provided by D. Cain, P. Chapman, A. Craig, S. N. Luoma, and S. Martin.

References

ANDERSON, R. V., AND J. E. BROWER. 1978. Patterns of trace metal accumulation in crayfish populations. Bull. Environ. Contam. Toxicol. 20: 120–127.

AOKI, Y., AND K. T. SUZUKI. 1984. Excretion of cadmium and change in the relative ratio of iso-cadmium-binding proteins during metamorphosis of fleshfly (*Sarcophaga peregrina*). Comp. Biochem. Physiol. 78C: 315–317.

AOKI, Y., K. T. SUZUKI, AND K. KUBOTA. 1984. Accumulation of cadmium and induction of its binding protein in the digestive tract of fleshfly (*Sarcophaga peregrina*) larvae. Comp. Biochem. Physiol. 77: 279–282.

BAGATTO, G., AND M. A. ALIKHAN. 1987. Copper, cadmium, and nickel accumulation in crayfish populations near copper–nickel smelters at Sudbury, Ontario, Canada. Bull. Environ. Contam. Toxicol. 38: 540–545.

BALLAN-DUFRANÇAIS, C. 1974. Accumulation minérales et pyriques chez trois espèces d'insectes Dictyoptères. Cellule 70: 315–330.

BENDELL-YOUNG, L., AND H. H. HARVEY. 1989. Concentrations and distribution of Fe, Zn and Cu in tissues of the white sucker (*Catostomus commersoni*) in relation to elevated levels of metals and low pH. Hydrobiologia 176/177: 349–354.

BRUNK, U., AND G. SKÖLD. 1967. The oxidation problem in the sulphide–silver method for histochemical demonstration of metals. Acta Histochem. 27: 199–206.

BRYAN, G. W. 1968. Concentrations of zinc and copper in the tissues of decapod crustaceans. J. Mar. Biol. Assoc. U.K. 48: 303–321.

BRYAN, G. W., AND L. G. HUMMERSTONE. 1978. Heavy metals in the burrowing bivalve *Scrobicularia plana* from contaminated and uncontaminated estuaries. J. Mar. Biol. Assoc. U.K. 58: 401–419.

CAIN, D. J., AND S. N. LUOMA. 1990. Influence of size and feeding habit on metal concentrations in aquatic insects. Abstr. No. 173, University of Georgia, Savannah R. Ecology Laboratory, Int. Conf. on Metals in Soil, Waters, Plants and Animals, Orlando, FL, USA.

CHAPMAN, R. F. 1984. Structure of the digestive system, p. 165–211. *In* G. A. Kerkut and L. I. Gilbert [ed.] Comprehensive insect physiology biochemistry and pharmacology. Vol. 4. Regulation: digestion, nutrition, excretion. Pergamon Press, Oxford, England.

CIBOROWSKI, J. J. H., AND L. D. CORKUM. 1988. Organic contaminants in adult aquatic insects of the St. Clair and Detroit rivers, Ontario, Canada. J. Great Lakes Res. 14: 148–156.

CLEMENTS, A. N. 1963. The physiology of mosquitoes. Pergamon Press, Oxford, England.

COUGHTREY, P. J., AND M. H. MARTIN. 1976. The distribution of Pb, Zn, Cd and Cu within the pulmonate mollusc *Helix aspera* Müller. Oecologia (Berlin) 23: 315–322.

DARLINGTON, S T., AND A. M. GOWER. 1990. Location of copper in larvae of *Plectrocnemia conspersa* (Curtis) (Trichoptera) exposed to elevated metal concentrations in a mine draingae stream. Hydrobiologia 196: 91–100.

DARLINGTON, S. T., A. M. GOWER, AND L. EBDON. 1987. Studies on *Plectrocnemia conspersa* (Curtis) in copper contaminated streams in south west England, p. 353–357. *In* M. Bournaud and H. Tachet [ed.] Proc. 5th Int. Symp. on Trichoptera. W. Junk Publ. Dordrecht, The Netherlands.

DOW, J. A. T. 1986. Insect midgut function. Adv. Insect Physiol. 19: 187–328.

ENGEL, D. W., M. BROUWER, AND F. P. THURBERG. 1985. Comparison of metal metabolism and metal-binding proteins in the blue crab and the American lobster, p. 229–245. *In* F. J. Vernberg, F. P. Thurberg, A. Calabrese, and W. Vernberg [ed.] Marine pollution and physiology: recent advances. B. W. Baruch Library in Marine Science 13.

FRICK, K. G., AND J. HERRMANN. 1990. Aluminum accumulation in a lotic mayfly at low pH — a laboratory study. Ecotoxicol. Environ. Saf. 19: 81–88.

GEORGE, S. G., J. A. NOTT, B. J. S. PIRIE, AND A. Z. MASON. 1976. A comparative quantitative study of cadmium retention in tissues of a marine bivalve during different fixation and embedding procedures. Proc. R. Microsc. Soc. (Micro '76 Suppl.) 11: 42.

HARE, L., P. G. C. CAMPBELL, A. TESSIER, AND N. BELZILE. 1989. Gut sediments in a burrowing mayfly (Ephemeroptera, *Hexagenia limbata*): their contribution to animal trace element burdens, their removal, and the efficacy of a correction for their presence. Can. J. Fish. Aquat. Sci. 46: 451–456.

HARE, L., E. SAOUTER, P. G. C. CAMPBELL, A. TESSIER, F. RIBEYRE, AND A. BOUDOU. 1991. Dynamics of cadmium, lead, and zinc exchange between nymphs of the burrowing mayfly *Hexagenia rigida* (Ephemeroptera) and the environment. Can. J. Fish. Aquat. Sci. 48: 39–47.

HUMBERT, W. 1977. The mineral concretions in the midgut of *Tomocerus minor* (Collembola): microprobe analysis and physioecological significance. Rev. Ecol. Biol. Sol 14: 71–80.

1978. Cytochemistry and X-ray microprobe analysis of the midgut of *Tomocerus minor* Lubbock (Insecta, Collembola) with special reference to the physiological significance of the mineral concretions. Cell Tissue Res. 187: 397–416.

JEANTET, A. Y., C. BALLAN-DUFRANÇAIS, AND R. MARTOJA. 1977. Insects resistance to mineral pollution. Importance of spherocrystal in ionic regulation. Rev. Ecol. Biol. Sol 14: 563–582.

JOHNSON, R. K. 1987. Seasonal variation in diet of *Chironomus plumosus* (L.) and *C. anthracinus* Zett. (Diptera: Chironomidae) in mesotrophic Lake Erken. Freshwater Biol. 17: 525–532.

KING, D. G., AND I. M. DAVIES. 1987. Laboratory and field studies of the accumulation of inorganic mercury by the mussel *Mytilus edulis* (L.). Mar. Pollut. Bull. 18: 40–45.

KOMNICK, H. 1977. Chloride cells and chloride epithelia of aquatic insects. Int. Rev. Cytol. 49: 285–329.

KORMONDY, E. J. 1965. Uptake and loss of zinc-65 in the dragonfly *Plathemis lydia*. Limnol. Oceanogr. 10: 427–433.

KRANTZBERG, G., AND P. M. STOKES. 1988. The importance of surface adsorption and pH in metal accumulation by chironomids. Environ. Toxicol. Chem. 7: 653–670.

1990. Metal concentrations and tissues distribution in larvae of *Chironomus* with reference to X-ray microprobe analysis. Arch. Environ. Contam. Toxicol. 19: 84–93.

LUOMA, S. N. 1983. Bioavailability of trace metals to aquatic organisms — A review. Sci. Total Environ. 28: 1–22.

MEYER, W., G. HARISCH, AND A. N. SAGREDOS. 1986. Biochemical and histochemical aspects of lead exposure in dragonfly larvae (Odonata: Anisoptera). Ecotoxicol. Environ. Saf. 11: 308–319.

NRCC. 1988. Biologically available metals in sediments. National Research Council of Canada, Assoc. Committee Sci. Criteria Environ. Quality, NRCC Publ. 27694. 298 p.

NYHOLM, N. E. I. 1981. Evidence of involvement of aluminum in causation of defective formation of eggshells and of impaired breeding in wild passerine birds. Environ. Res. 26: 363–371.

PHILLIPS, J. E., J. HANRAHAN, M. CHAMBERLIN, AND B. THOMSON. 1986. Mechanisms and control of readsorption in the insect hindgut. Adv. Insect Physiol. 19: 329–422.

PIERSON, M. 1956. Contribution à l'histologie de l'appareil digestif de *Chironomus plumosus* L. Ann. Sci. Nat. Zool. 11: 107–122.

RAY, S., D. W. MCLEESE, B. A. WAIWOOD, AND D. PEZZACK. 1980. The disposition of cadmium and zinc in *Pandalus montagui*. Arch. Environ. Contam. Toxicol. 9: 675–681.

ROBACK, S. S. 1976. Note on the feeding habits of *Clinotanypus pinguis* (Loew) (Diptera: Chironomidae: Tanypodinae). Entomol. News 87: 243–244.

SEIDMAN, L. A., G. BERGTROM, D. J. GINGRICH, AND C. C. REMSEN. 1986a. Accumulation of cadmium by the fourth instar larvae of the fly *Chironomus thummi*. Tissue & Cell 18: 395–405.

SEIDMAN, L. A., G. BERGTROM, AND C. C. REMSEN. 1986b. Structure of the larval midgut of the fly *Chironomus thummi* and its relationship to sites of cadmium sequestration. Tissue & Cell 18: 407–418.

SEPHTON, T. W. 1987. Some observations on the food of larvae of *Procladius bellus* (Diptera: Chironomidae). Aquat. Insects 9: 195–202.

SMOCK, L. A. 1983. Relationships between metal concentrations and organism size in aquatic insects. Freshwater Biol. 13: 313–321.

SOHAL, R. S., P. D PETERS, AND T. A. HALL. 1976. Fine structure and X-ray microanalysis of mineralized concretions in the Malpighian tubules of the housefly, *Musca domestica*. Tissue & Cell 8: 447–458.

STOBBART, R. H., AND J. SHAW. 1974. Salt and water balance; excretion, p. 361–446. *In* M. Rockstein [ed.] The physiology of Insecta. Vol. 5. 2nd ed. Academic Press, New York, NY.

SUMI, Y., T. SUZUKI, M. YAMAMURA, S. HATAKEYAMA, Y. SUGAYA, AND K. T. SUZUKI. 1984. Histochemical staining of cadmium taken up by the midge larva, *Chironomus yoshimatsui* (Diptera, Chironomidae). Comp. Biochem. Physiol. 79A: 353–357.

SUZUKI, K. T., Y. AOKI, M. NISHIKAWA, H. MASUI, AND F. MATSUBARA. 1984. Effect of cadmium-feeding on tissue concentrations of elements in germ-free silkworm (*Bombyx mori*) larvae and distribution of cadmium in the alimentary canal. Comp. Biochem. Physiol. 79C: 249–253.

TAPP, R. L., AND A. HOCKADAY. 1977. Combined histochemical and X-ray microanalytical studies on the copper-accumulating granules in the midgut of larval *Drosophila*. J. Cell Sci. 26: 201–215.

TERRA, W. R. 1990. Evolution of digestive systems of insects. Annu. Rev. Entomol. 35: 181–200.

TESSIER, A., P. G. C. CAMPBELL, J. C. AUCLAIR, AND M. BISSON. 1984. Relationships between the partitioning of trace metals in sediments and their accumulation in the tissues of the freshwater mollusc *Elliptio complanata* in a mining area. Can. J. Fish. Aquat. Sci. 41: 1463–1472.

TIMMERMANS, K. R., B. VAN HATTUM, M. H. S. KRAAK, AND C. DAVIDS. 1989. Trace metals in a littoral foodweb: concentrations in organisms, sediment and water. Sci. Total Environ. 87/88: 477–494.

UTHE, J. F., AND C. L. CHOU. 1987. Cadmium in sea scallop (*Placopecten magellanicus*) tissues from clean and contaminated areas. Can. J. Fish. Aquat. Sci. 44: 91–98.

WATERHOUSE, D. F. 1954. Occurrence and endodermal origin of the peritrophic membrane in some insects. Nature (Lond.) 172: 676–677.

WHITE, S. L., AND P. S. RAINBOW. 1984. Zinc flux in *Palaemon elegans* (Crustacea: Decapoda): moulting, individual variation and tissue distribution. Mar. Ecol. Prog. Ser. 19: 153–166.

Limits to Growth of Young-of-the-Year Walleye (*Stizostedion vitreum vitreum*): An Individual-Based Model Perspective

Charles P. Madenjian

Center for Limnology, University of Wisconsin, Madison, WI 53706, USA

Madenjian, C. P. 1991. Limits to growth of young-of-the-year walleye (*Stizostedion vitreum vitreum*): an individual-based model perspective. Can. J. Fish. Aquat. Sci. 48: 1492–1499.

An individual-based model (IBM) accurately described the variation in growth exhibited between young-of-the-year (YOY) walleye (*Stizostedion vitreum vitreum*) cohorts from Oneida Lake (New York) and western Lake Erie. The IBM was used to develop a general explanation for the wide variability in growth exhibited by YOY walleye. Length of growing season and encounter rate, λ, between YOY walleye and the prey fish set the potential for growth in a particular aquatic system. Walleye spawning observations and observed YOY prey densities in Oneida Lake versus those for western Lake Erie corroborated these modeling results. Given a specific encounter rate and length of growing season, first-year growth of walleye was further controlled by size of prey fish relative to YOY walleye size, availability of prey fish throughout the summer and early fall months, and water temperature.

Un modèle basé sur les individus (IBM) décrit de façon exacte la variation de croissance préservée par des cohortes de jeunes de l'année de dorés (*Stizostedion vitreum vitreum*) observés dans le lac Oneida (New York) et l'ouest du lac Érié. L'ordinateur IBM a été utilisé afin d'élaborer une explication générale pour la grande variabilité de croissance présentée par ces jeunes de l'année. La durée de la saison de croissance et le taux de rencontre, λ, entre les jeunes de l'année et les poissons qui leur servent de proies permettent d'établir le potentiel de croissance dans un système aquatique déterminé. Des observations du frai de dorés et les densités observées de proies de jeunes de l'année dans le lac Oneida, par rapport à celles de l'ouest du lac Érié, ont permis de corroborer les résultats de modélisation. Étant donné le taux particulier de rencontre et la durée de la saison de croissance, la croissance des dorés au cours de la première année dépendait en plus de la taille des poissons servant de proies par rapport à celle des jeunes de l'année, ainsi que la disponibilité des poissons servant de proies pendant l'été et le début de l'automne et enfin de la température de l'eau.

Received October 12, 1990
Accepted February 20, 1991
(JA755)

Reçu le 12 octobre 1990
Accepté le 20 février 1991

Walleye (*Stizostedion vitreum vitreum*) is one of the most valuable North American gamefish (Scott and Crossman 1973; Hushak et al. 1986). Yield from the fishery, whether it be commercial or sport, depends heavily on recruitment success. An important determinant of walleye recruitment success is first-year growth (Forney 1976).

Growth of young-of-the-year (YOY) walleye varies substantially both from year to year within a particular lake and between different lakes. In Oneida Lake (New York) from the years 1961 to 1977, average length of the YOY walleye cohort at the end of the growing season ranged from 120 to 180 mm (Forney 1978). In contrast, YOY walleye in the western basin of Lake Erie exhibited the highest growth reported (Regier et al. 1969). YOY walleye attained lengths of 230–260 mm during the early 1960's in western Lake Erie (Nepszy 1985; Hatch et al. 1987; Muth and Wolfert 1986). Average YOY length at the end of the growing season declined during the 1970's, yet YOY walleye populations still reached mean lengths of 185–220 mm during the late 1970's (Muth and Wolfert 1986).

Explanations for variation in YOY walleye growth within a particular lake have been offered (Forney 1966; Parsons 1971), but a general model that successfully accounts for both within-lake and between-lake variation has yet to be proposed. Parsons (1971) attributed the excellent growth of western Lake Erie walleye during 1959 to high abundance of prey fish. However, other factors also appeared to be important regulators of YOY walleye growth. Overall YOY prey fish abundance did not decline during the 1970's (Hayward and Margraf 1987), yet YOY walleye growth declined during that time. Composition of the YOY prey fish population shifted from a population dominated by spottail shiner (*Notropis hudsonius*) during the 1960's to a population dominated by gizzard shad (*Dorosoma cepedianum*) during the 1980's (Muth 1985). First-year gizzard shad grow considerably faster than YOY shiner, and most shad were too large to be consumed by YOY walleye by November during 1981 (Knight et al. 1984). To further confound matters, average length of the YOY walleye population in June (when first recruitment to the trawl occurred) declined during the 1970's and early 1980's in western Lake Erie (R. L. Knight, Ohio Department of Natural Resources, Lake Erie Fisheries Unit, Sandusky, OH, pers. comm.).

Forney (1966) concluded that much of the year-to-year variability in YOY walleye growth in Oneida Lake could not be explained by YOY yellow perch (*Perca flavescens*, the principal prey species for walleye in the lake) density alone. Rather, much of year-to-year variability in YOY walleye growth was attributed to size of YOY yellow perch relative to YOY walleye size (Forney 1966). If perch were too large to be vulnerable to predation by YOY walleye, then walleye growth would be expected to be slow because their major sustenance would be from invertebrate prey. Growth was more rapid when YOY walleye fed on fish rather than invertebrates (Forney 1966).

Undoubtedly many other factors impinge on YOY walleye growth. For example, during some years in Oneida Lake the YOY perch population was severely depleted by midsummer (Forney 1980; Mills et al. 1987). Consequently, consumption of perch by walleye was substantially reduced for the remainder of the growing season. According to Hokanson and Koenst (1986), water temperature will also influence growth of YOY walleye, with the optimum temperature for growth being 26°C.

Madenjian and Carpenter (1991) developed an individual-based model (IBM) for growth of YOY walleye. The model incorporated essential features of the predator–prey interaction at the level of the individual, and included bioenergetic constraints. The model accurately predicted length–frequency distributions of the YOY walleye cohort at the end of the growing season in Oneida Lake and Lake Mendota (Wisconsin).

In the present study, the IBM was applied to Oneida Lake and western Lake Erie in order to explain the variation in YOY walleye growth rates displayed between and within these systems. The IBM was used to identify which factors were most important in limiting YOY growth and to propose a general scheme for regulation of YOY walleye growth. Application of the IBM to western Lake Erie populations provided insight into the high first-year growth of walleye in this region. Finally, the model was applied to the western Lake Erie system to determine whether the decrease in average length at the start of the sampling season or the increasing proportion of gizzard shad in the prey fish population was the key factor leading to the decline in YOY walleye growth during the 1970's.

Although growth comparisons between the different aquatic systems were based on mean length of the YOY walleye cohort at the end of the growing season, an IBM approach appeared more appropriate than an aggregated model approach. The IBM has been shown to accurately describe growth of YOY largemouth bass (*Micropterus salmoides*) in a Tennessee reservoir (Adams and DeAngelis 1987) and growth of YOY walleye in Oneida Lake and Lake Mendota (Madenjian and Carpenter 1991). Above-mentioned studies on Oneida Lake have indicated that interactions between YOY walleye and prey fish at the level of the individual should be considered in describing YOY walleye growth; and IBMs explicitly account for these predator–prey interactions at an individual level.

Model

The IBM for YOY walleye growth is a computer simulation model in which a set of individuals representing the population are tracked over the growing season (see Adams and DeAngelis (1987) and Huston et al. (1988) for background to IBMs). During each day of the simulation, a walleye encountered prey fish at a rate determined by a Poisson-distributed random variable with mean equal to λ (Fig. 1). If the prey fish was sufficiently small to be ingested, i.e. the ratio of length of prey fish and walleye length was less than γ, and if the consumption of the prey fish did not exceed the maximum daily limit on consumption, then the prey fish was ingested. All fish lengths reported in this paper are total lengths. Maximum daily consumption was described as a function of walleye weight and water temperature (Madenjian and Carpenter 1991). Optimal water temperature for consumption by YOY walleye was assigned the value of 26°C (Hokanson and Koenst 1986).

If the individual walleye did not consume any prey fish on a particular day, then that individual received a ration of invertebrate food equivalent to a fraction α of the maximum daily consumption permitted (Fig. 1); α was set equal to 0.3 (Madenjian and Carpenter 1991). Daily weight gained by the walleye was equal to the product of gross growth efficiency (gge) and biomass consumed; gge was set equal to 0.25 (Madenjian and Carpenter 1991), the value used by Adams and DeAngelis (1987) for their IBM describing growth of YOY largemouth bass.

Growth of YOY walleye was simulated from early or mid-summer (depending on the available data) to the end of the growing season in late October or early November. At the end of the simulation run, the length–frequency distribution and mean total length for the YOY cohort were computed. See Madenjian and Carpenter (1991) for more details on the IBM.

IBM Application

For each IBM application, growth of 500 YOY walleye was simulated from June or July to late October or early November. The length–frequency distribution of the simulated YOY walleye cohort at the end of the growing season was plotted, and mean total length of the cohort was recorded. Encounter rate was adjusted to yield a close fit between predicted and observed YOY walleye length–frequency distributions (see Madenjian and Carpenter 1991). Size-selective mortality was not considered in the simulations. Results from IBM applications presented in this paper suggested that size-selective mortality has minimal impact on the size distribution of the YOY walleye cohort (see Results and Discussion sections).

Oneida Lake

IBMs published to date have employed a constant encounter rate over the growing season (Adams and DeAngelis 1987; Madenjian and Carpenter 1991). I tested that assumption by comparing mean total lengths of the YOY walleye cohort observed at various stages of the growing season with predicted mean length of YOY walleye. During 1975, walleye size was so much larger than perch size in Oneida Lake that perch were highly vulnerable to predation by YOY walleye. During 1977, perch showed an intermediate level of vulnerability to predation by YOY walleye.

Western Lake Erie

Whereas yellow perch was the predominant prey species for YOY walleye in Oneida Lake during 1975 and 1977, diet in western Lake Erie included yellow perch, spottail shiner, and emerald shiner (*Notropis atherinoides*) during the 1959 growing season (Parsons 1971). To simplify the model, populations of the two shiner species were pooled because growth schedules of the two species were similar (Parsons 1971). I simulated growth of the 1959 YOY walleye cohort using the growth schedules provided by Parsons (1971) for each of the two prey groups: shiners and yellow perch. Water temperatures throughout the 1959 growing season were not available; however, 1959 was reported as a relatively warm year (Beeton 1963). Hence, the water temperatures observed by Chandler (1944) in western Lake Erie for the 1941 growing season, another relatively warm summer in Lake Erie, were used. Initial size distribution of the YOY walleye was taken from Parsons (1971). The maximum ratio of prey length to walleye length at which the prey was considered still vulnerable to predation, γ, was set equal to 0.46 for both prey groups. This was a reasonable estimate for all prey species based on the findings of Knight et al. (1984).

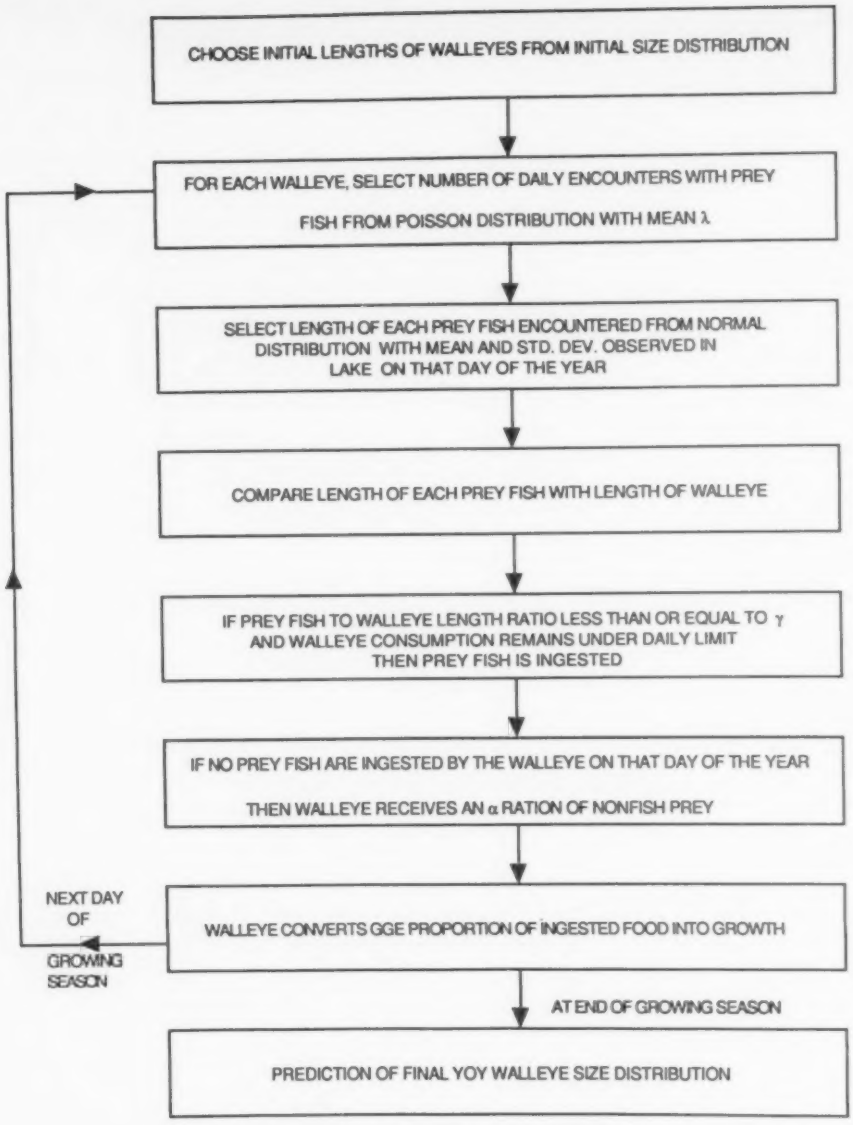

CHOOSE INITIAL LENGTHS OF WALLEYES FROM INITIAL SIZE DISTRIBUTION
FOR EACH WALLEYE, SELECT NUMBER OF DAILY ENCOUNTERS WITH PREY FISH FROM POISSON DISTRIBUTION WITH MEAN λ
SELECT LENGTH OF EACH PREY FISH ENCOUNTERED FROM NORMAL DISTRIBUTION WITH MEAN AND STD. DEV. OBSERVED IN LAKE ON THAT DAY OF THE YEAR
COMPARE LENGTH OF EACH PREY FISH WITH LENGTH OF WALLEYE
IF PREY FISH TO WALLEYE LENGTH RATIO LESS THAN OR EQUAL TO γ AND WALLEYE CONSUMPTION REMAINS UNDER DAILY LIMIT THEN PREY FISH IS INGESTED
IF NO PREY FISH ARE INGESTED BY THE WALLEYE ON THAT DAY OF THE YEAR THEN WALLEYE RECEIVES AN α RATION OF NONFISH PREY
NEXT DAY OF GROWING SEASON
WALLEYE CONVERTS GGE PROPORTION OF INGESTED FOOD INTO GROWTH
AT END OF GROWING SEASON
PREDICTION OF FINAL YOY WALLEYE SIZE DISTRIBUTION

FIG. 1. Diagram of the IBM for growth of YOY walleye.

YOY walleye preferred shiners over perch (Knight et al. 1984). Consequently, encounters with shiners were processed before perch encounters in the IBM simulations. A similar procedure was tested and found adequate for modeling walleye prey preferences in Lake Mendota (Madenjian and Carpenter 1991).

Encounter rates (λ_{SH} for shiners and λ_{YP} for yellow perch) were adjusted so that mean length of the predicted cohort matched that for the observed 1959 cohort at the end of the growing season. Encounter rates were compared between Oneida Lake and western Lake Erie applications. Furthermore, the predicted time course of cohort mean length was compared with mean length observed over the course of the growing season in order to find any abrupt changes in growth rate during the growing season.

For analysis of the 1981 western Lake Erie system, gizzard shad was added to the list of prey groups because of its prominence both in trawl catches and in walleye diet during that year. Because overall YOY prey abundance during the 1980's was not believed to be different than in 1959 (Hayward and Margraf 1987), the sum of encounter rates for the 1981 run ($\lambda_{SH} + \lambda_{YP} + \lambda_{GS}$) was assumed equal to the sum of the encounter rates for the 1959 simulation. Gizzard shad comprised between 55 and 95% of the pooled shiner–perch–shad population in western Lake Erie during 1981 (Muth 1985; Nepszy 1985). The proportion of encounters with gizzard shad of the total encounters with prey was adjusted until predicted mean length of the YOY walleye cohort at the end of the growing season equalled the observed mean length. Remaining encounters were split between the shiners and perch in the same ratio as for 1959. Growth schedules of shiners, yellow perch, and

gizzard shad were taken from Knight et al. (1984) and R. L. Knight (pers. comm.). The 1981 temperature regime for western Lake Erie was taken from Hayward and Margraf (1987).

YOY walleye were assumed to prefer shiners and shad over yellow perch (Knight et al. 1984), but no preference was assumed between gizzard shad and shiners. Thus, for a particular walleye individual on a particular day of the growing season, number of encounters with an aggregated population of shad and shiners was determined by randomly selecting from a Poisson distribution with mean equal to $\lambda_{SH} + \lambda_{GS}$. Then the prey group (shiners or gizzard shad) for each of the encounters was determined at random, based on percentage of total number of encounters for each of the two prey groups. Perch encounters were processed after the shiner and shad encounters. Simulations in which preference was given to either shiners or shad resulted in predicted growth similar to that from the simulation in which no preference was assumed.

Length–weight relationships for spottail and emerald shiners were similar (Carlander 1969), and the relationship for spottail shiner was used for the "shiner" population in the IBM simulations. The length–weight function for gizzard shad furnished by Bodola (1966) was used in the 1981 simulation run.

Additional Simulations

To assess the effect of water temperature on differences in growth between Oneida Lake and western Lake Erie, temperature regimes were exchanged between the 1959 Lake Erie and 1975 Oneida Lake simulations. That is, the 1959 Lake Erie simulation was repeated with all parameters and initial conditions identical to the original run, except that the 1975 Oneida Lake temperature regime was substituted for the observed temperature regime in western Lake Erie during 1959. Similarly, the 1975 Oneida Lake simulation, but under the 1959 western Lake Erie temperature regime, was performed.

To assess the effect of encounter rate on differences in growth between the two lakes, encounter rates were exchanged between the two lakes. Finally, in order to determine if the high abundance of gizzard shad had an important effect on YOY walleye growth during 1981, the 1981 simulation was modified such that all of the encounters with gizzard shad were converted to encounters with shiners.

Results

Oneida Lake

YOY walleye typically averaged between 20 and 35 mm in length by 15 June in Oneida Lake (Forney 1966). In 1975 and 1977, mean lengths of the YOY walleye cohorts were 30 and 25 mm, respectively, at mid-June.

Assigning λ equal to 4.1 encounters·d^{-1} (for an individual walleye) for the 1975 Oneida Lake simulation resulted in a predicted length–frequency distribution that was in close agreement with the observed distribution (Madenjian and Carpenter 1991). However, the predicted mean length of the YOY walleye cohort was less than the observed mean length for much of the growing season (Fig. 2). Observed growth rate decreased abruptly in early September (day 254); after day 254, predicted mean length approached observed mean length.

Because of the abrupt change in YOY walleye growth during the 1975 season, the IBM was fitted to allow for two different encounter rates: λ_1, from day 211 (30 July) to day 253 (10 September) and λ_2 from day 254 (11 September) to day 290 (17 October). λ_1 and λ_2 were adjusted to give an adequate fit to the observed length–frequency for YOY walleye at the end of the growing season, while accounting for the rapid growth early in the growing season (Fig. 2). λ_1 and λ_2 were estimated as 11.0 and 0.6 encounters·d^{-1}, respectively. Predicted size distribution of the YOY walleye cohort at the end of the growing season matched the observed distribution fairly closely (Fig. 3). When λ was held constant at 11.0 encounters·d^{-1} throughout the growing season, predicted YOY walleye mean length was 195 mm, about 16 mm greater than that predicted by the model when λ was 4.1 encounters·d^{-1}.

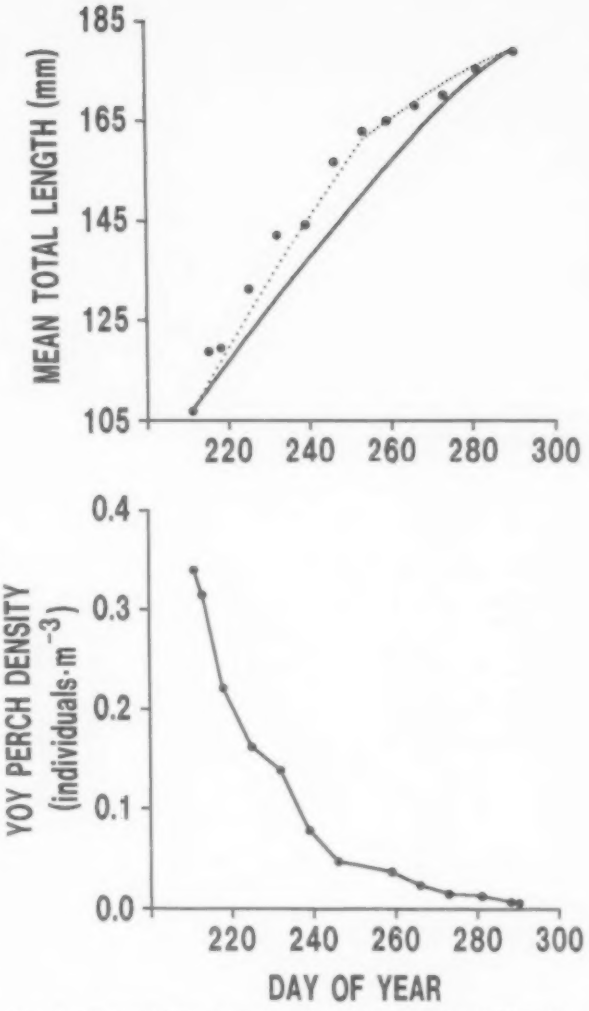


FIG. 2. Observed (●) and predicted mean length of the YOY walleye population in Oneida Lake during 1975. Predictions were based on an IBM, assuming a constant prey encounter rate throughout the growing season (solid line) and assuming a change in prey encounter rate on day 254 (dotted line). Also plotted was density of YOY yellow perch in Oneida Lake during 1975 (taken from Mills et al. 1987).

The rapid growth by YOY walleye followed by a decline in early fall corresponded with a precipitous decline in YOY yellow perch abundance followed by a period of low YOY yellow perch density (Fig. 2). YOY perch density remained

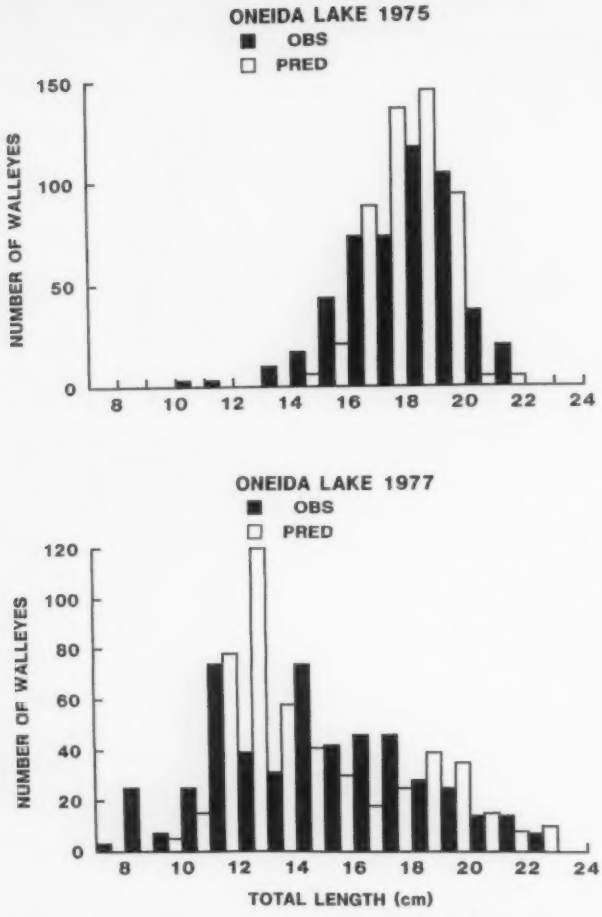


FIG. 3. Observed (OBS) and predicted (PRED) length–frequency distributions of YOY walleye at the end of the 1975 and 1977 growing seasons in Oneida Lake. Predictions were based on an IBM, assuming a change in prey encounter rate during the 1975 season and assuming a constant prey encounter rate throughout the 1977 season.

below 0.03 individuals·m^{-3} from early September through late October.

The observed YOY walleye size distribution at the end of the 1977 growing season was similar to the predicted distribution when encounter rate was set equal to 7.2 encounters·d^{-1} (Fig. 3). YOY walleye growth was considerably slower in 1977 than in 1975; average mean length was almost 180 mm in 1975 in comparison with less than 150 mm at the end of the 1977 season. Predicted mean length of the YOY walleye cohort accurately tracked observed mean length throughout the season (Fig. 4). YOY perch density during 1977 did not show a steep decline, as in 1975. The 1977 decline was gradual, and density never dropped below 0.04 individuals·m^{-3} (Fig. 4).

Western Lake Erie

In contrast with Oneida Lake populations, mean length of the YOY walleye population in western Lake Erie was 20–75 mm by mid-June (R. L. Knight, pers. comm.). Estimated mean lengths were 63.5 and 24 mm in 1959 and 1981, respectively.

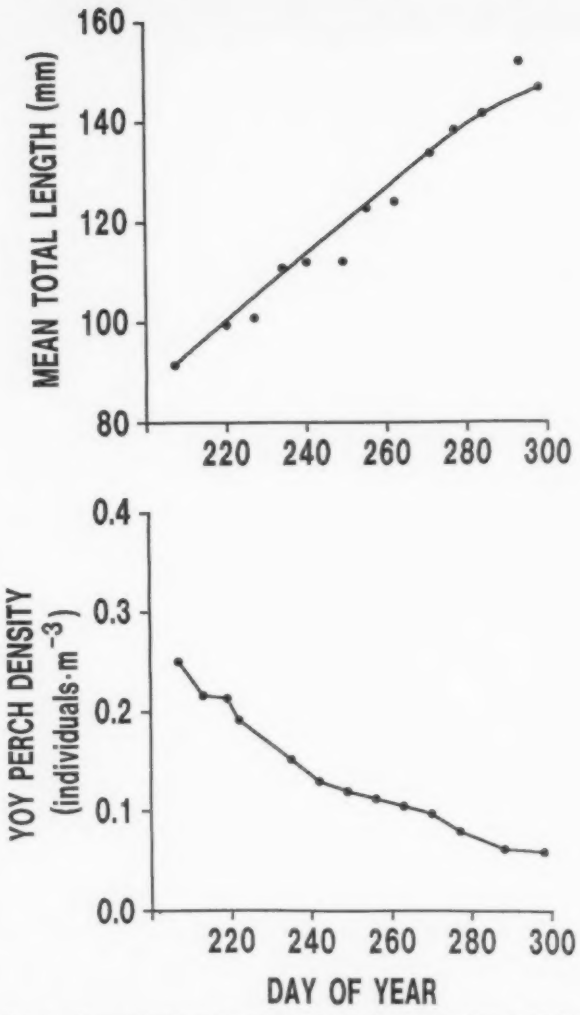


FIG. 4. Observed (●) and predicted (solid line) mean length of the YOY walleye population in Oneida Lake during 1977. Predictions were based on an IBM, assuming a constant prey encounter rate throughout the growing season. Also plotted was density of YOY perch in Oneida Lake during 1977 (taken from Mills et al. 1987).

Predicted mean length of YOY walleye matched the observed mean length at the end of the 1959 growing season when λ_{SH} and λ_{YP} were set equal to 30 and 15 encounters·d^{-1}, respectively. Thus, overall daily encounter rate for an individual walleye was 45 encounters·d^{-1}. Observed and predicted mean lengths were in fairly close agreement throughout the 1959 season (Fig. 5). YOY prey fish remained relatively abundant throughout the 1959 season (Parsons 1971).

Predicted 1981 YOY walleye sizes fit the observed mean lengths well (Fig. 6). Predicted mean length of the YOY cohort in November matched the observed average length of 199 mm when gizzard shad accounted for 86.7% of the simulated prey population. Hence, λ_{GS}, λ_{SH}, and λ_{YP} were equal to 39, 4, and 2 encounters·d^{-1}, respectively. Observed prey abundance did not exhibit any drastic declines during the growing season (Fig. 6).

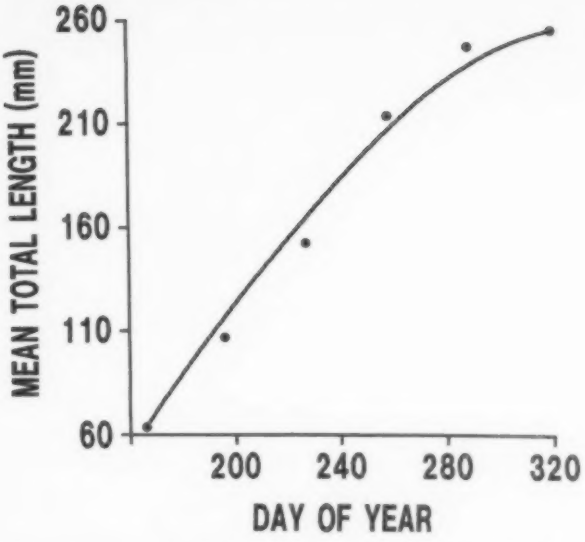


FIG. 5. Observed (•) and predicted (solid line) mean length of the YOY walleye population in western Lake Erie during 1959. Predictions were based on an IBM, assuming a constant prey encounter rate throughout the growing season.

Rates of growth were remarkably similar during 1959 and 1981. During 1959, the observed average length of the YOY walleye cohort was 63.5 mm on June 15 whereas the 1981 walleye cohort was predicted to reach an average length of 63.5 mm on 8 July. At an average length of 63.5 mm, instantaneous rates of growth were 1.66 and 1.70 mm·d^{-1} during 1959 and 1981, respectively. Furthermore, daily growth rates averaged over the 1959 and 1981 growing seasons were similar at 1.25 and 1.21 mm·d^{-1}, respectively.

Additional Simulations

When the Lake Erie encounter rate (45 encounters·d^{-1}) was substituted for the Oneida Lake rate (4.1 encounters·d^{-1}) in the 1975 Oneida Lake simulation, average size of YOY walleye at the end of the growing season increased from 179 to 214 mm (Table 1). Substituting encounter rates of 4.1 and 7.2 encounters·d^{-1} for the overall λ in the 1959 Lake Erie simulation resulted in a decrease in average YOY size from 254 to 206 and 229 mm, respectively.

Western Lake Erie, with an average water temperature of 21.1°C for the period 1 August through 15 October (Grumblatt 1976), was slightly warmer than Oneida Lake (approximately 20°C) over that same period. When the 1975 Oneida Lake temperature regime was employed in the 1959 Lake Erie simulation, predicted mean length of the YOY at the end of the growing season decreased slightly from 254 to 246 mm (Table 1). Similarly, predicted mean length of the simulated 1975 year class in Oneida Lake showed just a slight increase from 179 to 191 mm when the converse scenario was used.

Replacement of gizzard shad encounters with shiner encounters had little impact on YOY walleye growth during 1981 in western Lake Erie (Table 1).

Discussion

Oneida Lake walleye spawn in April (Forney 1966). Larval walleyes have been collected in Oneida Lake from the second

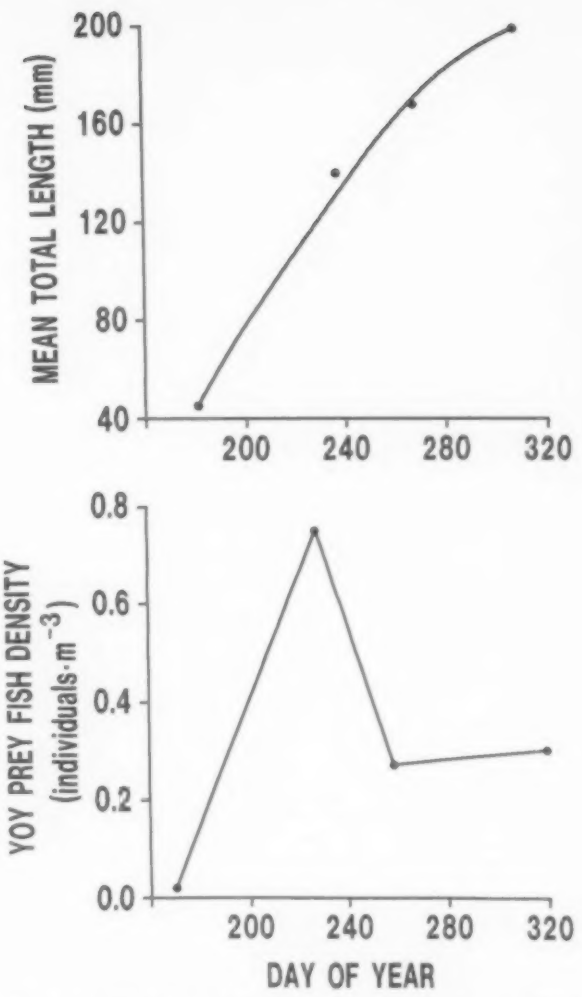


FIG. 6. Observed (•) and predicted (solid line) mean length of the YOY walleye population in western Lake Erie during 1981. Predictions were based on an IBM, assuming a constant prey encounter rate throughout the growing season. Also plotted was density of YOY prey fish in western Lake Erie during 1981 (derived from Knight et al. 1984, based on number of fish per trawl and estimated volume swept per trawl haul).

week in May through the second week in June. Newly hatched larvae were collected in early May. By mid-June, YOY walleye averaged 30 mm in length. In contrast, larval fish collections from tributaries to western Lake Erie indicated that some western Lake Erie walleyes move into tributaries and spawn during March. Cooper et al. (1981) observed larval walleye in the Maumee and Sandusky river estuaries of western Lake Erie from the second week in April through the third week in May. Walleye have also been observed spawning in western Lake Erie proper during April (Regier et al. 1969). Perhaps in some years, such as 1959, the river-spawned stock contributed the major portion of the lake population of YOY walleye. A YOY walleye population dominated by river-spawned individuals would explain the larger size of YOY walleye by mid-June in western Lake Erie during 1959 compared with Oneida Lake.

TABLE 1. Effects of exchanging temperature regimes and prey encounter rates between the 1959 western Lake Erie and 1975 Oneida Lake systems on YOY walleye growth. Also included is the effect of converting encounters with shad to encounters with shiners on growth of YOY walleye in western Lake Erie during 1981. Effects on average total length of the YOY walleye population in fall were determined via IBM simulations. N/A = not applicable.

	Average total length (mm) of YOY walleye cohort in fall			
Lake system	Observed length	Exchanged temperature regime	Exchanged encounter rate	Shad converted to shiner encounters
Oneida Lake, 1975	179	191	214	N/A
Western Lake Erie,1959	254	246	206	N/A
Western Lake Erie, 1981	199	N/A	N/A	212

Of course, an earlier spawning allowed for a longer growing season.

According to the IBM applications, YOY walleye encountered YOY prey individuals with a much higher frequency in western Lake Erie than in Oneida Lake. Maximum λ fitted to Oneida Lake populations was 7.2 encounters·d^{-1}, as opposed to 45 encounters·d^{-1} in western Lake Erie applications. These results from the IBM applications were supported by field observations on the absolute abundances of prey populations in both lakes. Highest density of yellow perch (by far the most abundant prey species) larvae observed in Oneida Lake from 1971 through 1977 was 5.3 individuals·m^{-3} sampled in spring 1975 (Mills et al. 1987). Jude et al. (1986) estimated gizzard shad densities as high as 59 individuals·m^{-3} during early June 1982 in western Lake Erie. This dramatic difference in abundances was maintained throughout the growing season. Of the years 1971–77, YOY yellow perch density on 15 October in Oneida Lake was highest in 1977 at a value of 0.06 individuals·m^{-3}. In contrast, abundance of the YOY prey population, as estimated by bottom trawl, in mid-October 1981 in western Lake Erie was 0.27 individuals·m^{-3} (Knight et al. 1984).

There was no evidence from the IBM applications that size-selective mortality played a major role in determining size distribution of YOY walleyes. Size-selective mortality was not included in any of the simulation runs, yet the IBM not only yielded adequate predictions of YOY walleye length–frequency distribution at the end of the growing season, but also forecasted average growth of YOY walleye populations reasonably well throughout the growing season. Furthermore, size-selective mortality need not be invoked to explain the abrupt change in the 1975 Oneida Lake growth curve for YOY walleye; rather, a decrease in encounter rate with YOY perch, corresponding to a precipitous drop in perch abundance, was sufficient to explain this peculiarity.

Most of the year-to-year variability in YOY walleye growth in Oneida Lake was due to vulnerability of the prey to predation by walleyes. Despite higher perch abundance in Oneida Lake during 1977 compared with 1975, YOY walleye were more than 30 mm longer, on the average, at the end of the 1975 growing season than in 1977. YOY yellow perch were considerably more susceptible, based on predator–prey size ratios, to predation by the majority of YOY walleye individuals constituting the population during the 1975 season than during the 1977 season (Forney 1978).

I propose that the decrease in YOY walleye growth from the early 1960's to the early 1980's in western lake Erie was chiefly due to a decrease in size of YOY walleye in June, rather than a shift in prey species composition. One possible explanation for the decrease in June size of YOY walleye was a declining contribution of the river-spawned stock to the YOY walleye population in western Lake Erie. Perhaps a shift occurred during the early 1970's in which the populations of YOY walleye in western lake Erie became dominated by lake-spawned individuals rather than tributary-spawned individuals. Water levels in Lake Erie were high during the 1970's and 1980's, which probably provided additional lake spawning habitats and improved existing spawning habitats (R. L. Knight, pers. comm.). Thus, if river-spawned recruitment remained constant while lake recruitment increased during this time, the result would be an increase in the relative contribution of lake-spawned walleye to the YOY population.

Another explanation for the decrease in June size of YOY walleye during the 1970's in western lake Erie would be that YOY walleye growth rate prior to June declined during the 1970's. However, there was no evidence to support this hypothesis. Instantaneous growth rates were nearly identical in early summer during 1959 and 1981. Abundances of zooplankton and small-sized benthic invertebrates, alternative food sources for walleye larvae, did not decline during the 1970's in western Lake Erie (Hayward and Margraf 1987). During June through November, when vulnerable to the trawl, YOY walleye in western Lake Erie fed almost exclusively on fish (Parsons 1971; Knight et al. 1984). Walleye larvae as small as 11 mm in total length are capable of preying on fish (Li and Mathias 1982). Again, prey fish abundance is believed to have remained relatively stable during the last 30 yr in western Lake Erie (K. M. Muth, U.S. Fish and Wildlife Service, Sandusky Biological Station, Sandusky, OH, pers. comm.).

Based on the IBM applications presented here, I propose the following scheme for limits to YOY walleye growth. Length of growing season and encounter rate λ, which is directly related to prey abundance (Madenjian and Carpenter 1991), set the potential for growth in a natural aquatic system. The remarkably high growth that has been observed in western Lake Erie appeared to be due to a combination of early walleye spawning and an abundance of prey fish. Given a length of the growing season and a particular λ, much of the remaining variation in YOY walleye growth could be explained by size of prey fish relative to YOY walleye throughout the course of the growing season. If prey fish growth was such that prey fish were too large to be vulnerable to predation, then YOY walleye growth would be relatively slow because invertebrates would dominate the diet. However, if prey fish growth was slow enough such that the bulk of the prey population was vulnerable to predation throughout the growing season, then YOY walleye would exhibit fast growth. Other factors influencing YOY walleye

growth include a severe depletion of prey fish abundance during the growing season (as was the case in Oneida Lake during 1975) and water temperature.

Acknowledgements

J. L. Forney is gratefully acknowledged for providing growth data on walleye and yellow perch from Oneida Lake. R. L. Knight and K. M. Muth kindly supplied walleye and prey species growth data for western Lake Erie. Special thanks to R. L. Knight for his ideas and insights on Lake Erie walleye growth. The manuscript was greatly improved from reviews by S. R. Carpenter, B. M. Johnson, R L. Knight, and P. R. Leavitt. This work was funded, in part, by the University of Wisconsin Sea Grant Institute under grants from the National Sea Grant College Program, National Oceanic and Atmospheric Administration, U.S. Department of Commerce, and from the State of Wisconsin. Federal grant NA90AA-D-SG469, project R/MW-41. The research was also supported by a Guyer Postdoctoral Fellowship granted to the author from the Department of Zoology at the University of Wisconsin.

References

ADAMS, S. M., AND D. L. DEANGELIS. 1987. Indirect effects of early bass–shad interactions on predator population structure and food web dynamics, p. 103–117. *In* W. C. Kerfoot and A. Sih [ed.] Predation: direct and indirect impacts on aquatic communities. University Press of New England, Hanover, NH.

BEETON, A. M. 1963. Limnological survey of Lake Erie 1959 and 1960. Great Lakes Fish. Comm. Tech. Rep. 6: 32 p.

BODOLA, A. 1966. Life history of the gizzard shad, *Dorosoma cepedianum* (Le Sueur), in western Lake Erie. Fish. Bull. 65: 391–425.

CARLANDER, K. D. 1969. Handbook of freshwater fishery biology. Vol. I. Iowa State University Press, Ames, IA. 752 p.

CHANDLER, D. C. 1944. Limnological studies of western Lake Erie. IV. Relation of limnological and climatic factors to the phytoplankton of 1941. Trans. Am. Microsc. Soc. 63: 203–236.

COOPER, C. L., W. C. BARTHOLOMEW, C. E. HERDENDORF, J. M. REUTTER, AND F. L. SNYDER. 1981. Limnetic larval fish of the Maumee and Sandusky river estuaries. J. Great Lakes Res. 7: 51–54.

FORNEY, J. L. 1966. Factors affecting first-year growth of walleyes in Oneida Lake, New York. N.Y. Fish Game J. 13: 146–167.

1976. Year-class formation in the walleye (*Stizostedion vitreum vitreum*) population of Oneida Lake, New York, 1966–73. J. Fish. Res. Board Can. 33: 783–792.

1978. Analysis of year-class formation in a walleye population. New York Federal Aid Fish and Wildlife Restoration Project F-17-R (final report for Job I-a). New York State Department of Environmental Conservation, Albany, NY.

1980. Evolution of a management strategy for the walleye in Oneida Lake, New York. N.Y. Fish Game J. 27: 105–141.

GRUMBLATT, J. L. 1976. Great Lakes water temperatures, 1966–1975. NOAA Tech. Memo. ERL GLERL-11-1: 127 p.

HATCH, R. W., S. J. NEPSZY, K. M. MUTH, AND C. T. BAKER. 1987. Dynamics of the recovery of the western Lake Erie walleye (*Stizostedion vitreum vitreum*) stock. Can. J. Fish. Aquat. Sci. 44(Suppl. 2): 15–22.

HAYWARD, R. S., AND F. J. MARGRAF. 1987. Eutrophication effects on prey size and food available to yellow perch in Lake Erie. Trans. Am. Fish. Soc. 116: 210–223.

HOKANSON, K. E. F., AND W. M. KOENST. 1986. Revised estimates of growth requirements and lethal temperature limits of juvenile walleyes. Prog. Fish-Cult. 48: 90–94.

HUSHAK, L. J., G. W. MORSE, AND K. K. APRAKU. 1986. Regional impacts of fishery allocation to sport and commercial interests: a case study of Ohio's portion of Lake Erie. N. Am. J. Fish. Manage. 6: 472–480.

HUSTON, M., D. DEANGELIS, AND W. POST. 1988. New computer models unify ecological theory. BioScience 38: 682–691.

JUDE, D. J., P. J. MANSFIELD, S. F. DEBOE, AND F. J. TESAR. 1986. Spatial distribution of entrained fish larvae in a power plant discharge canal. Can. J. Fish. Aquat. Sci. 43: 1070—1074.

KNIGHT, R. L., F. J. MARGRAF, AND R. F. CARLINE. 1984. Piscivory by walleyes and yellow perch in western Lake Erie. Trans. Am. Fish. Soc. 113: 677–693.

LI, S., AND J. A. MATHIAS. 1982. Causes of high mortality among cultured larval walleyes. Trans. Am. Fish. Soc. 111: 710–721.

MADENJIAN, C. P., AND S. R. CARPENTER. 1991. Individual-based model for growth of young-of-the-year walleye: a piece of the recruitment puzzle. Ecol. Appl. 1: 268–279.

MILLS, E. L., J. L. FORNEY, AND K. J. WAGNER. 1987. Fish predation and its cascading effect on the Oneida Lake food chain, p. 118–131. *In* W. C. Kerfoot and A. Sih [ed.] Predation: direct and indirect impacts on aquatic communities. University Press of New England, Hanover, NH.

MUTH, K. M. 1985. Changes in prey fish abundance in western Lake Erie during periods of high and low predator abundance, p. 27–38. *In* R. L. Eshenroder [ed.] Presented papers from the Council of Lake Committees Plenary Session on Great Lakes predator–prey issues, March 20, 1985. Great Lakes Fish. Comm. Spec. Publ. 85-3.

MUTH, K. M., AND D. R. WOLFERT. 1986. Changes in growth and maturity of walleyes associated with stock rehabilitation in western Lake Erie, 1964–1983. N. Am. J. Fish. Manage. 6: 168–175.

NEPSZY, S. J. 1985. Walleye in western Lake Erie: responses to change in predators and prey, p. 57–76. *In* R. L. Eshenroder [ed.] Presented papers from the Council of Lake Committees Plenary Session on Great Lakes predator–prey issues, March 20, 1985. Great Lakes Fish. Comm. Spec. Publ. 85-3.

PARSONS, J. W. 1971. Selective food preferences of walleyes of the 1959 year class in Lake Erie. Trans. Am. Fish. Soc. 100: 474–485.

REGIER, H. A., V. C. APPLEGATE, AND R. A. RYDER. 1969. The ecology and management of the walleye in western Lake Erie. Great Lakes Fish. Comm. Tech. Rep. 15: 101 p.

SCOTT, W. B., AND E. J. CROSSMAN. 1973. Freshwater fishes of Canada. Bull. Fish. Res. Board. Can. 184: 966 p.

State of the Lake Ontario Ecosystem: Introduction to an Ecosystem Perspective on a Vital Resource

Joseph V. DePinto

Great Lakes Program, State University of New York at Buffalo, 207 Jarvis Hall, Buffalo, NY 14260, USA

(JB018)

In an inventory of the large lakes of the world, Herdendorf (1982) identified 253 large lakes with a surface area of 500 km^2 or greater. Collectively, these 253 lakes (189 are freshwater systems) account for 93% of the total surface area and 88% of the total volume of water held in the world's lakes. The Laurentian Great Lakes include the three largest natural freshwater lakes in North America and contain over 20% of the world's surface freshwater (22 800 km^3). The Great Lakes basin, which covers over 766 000 km^2 of land and water on the U.S.–Canadian border, is home to an estimated 8 million Canadians (approximately 50% of the population) and 28 million Americans (approximately 15% of the population). We rely on this magnificent economic and aesthetic resource for our water supplies (serves over 26 million people within the basin), recreation and tourism ($8–12 billion per year), transportation (over 50 million tons of commercial cargo pass through the St. Lawrence River annually), hydroelectric power generation (over 40 billion kilowatt hours in the United States and Canada), a wide variety of industrial and manufacturing uses (over 13 000 plants located within the basin), and, of course, for waste assimilation.

Along with the key roles that large lakes play in the economy and general well-being of those living within their basin comes the need to deal with the many unique and complex problems that tend to plague these systems. Perhaps the most prominent among these problems today is the entry and subsequent effects of persistent toxic chemicals. While this problem is certainly ubiquitous (over 30 000 chemicals currently in commercial use, approximately 1000 new chemicals are developed each year, and over 1000 chemicals are suspected carcinogens), large lakes have special characteristics related to their size, hydrology, ecology, and human exploitation that exacerbate the problem. The International Joint Commission (IJC) has confirmed that over 350 toxic chemicals have been measured at least once in the Great Lakes basin.

The Great Lakes research and resource management community recognized the severity of the toxic chemical problem in its 1978 revision of the Great Lakes Water Quality Agreement, first signed by the Governments of Canada and the United States in 1972. Subsequently, the IJC as well as State, Provincial, and National Research/Regulatory Agencies have initiated numerous research and management programs intended to understand and effectively manage toxic substances in the Great Lakes. Through programs such as PLUARG (Pollution from Land Use Activities Reference Group), the Great Lakes "Areas of Concern" Remedial Action Plans, and the Upper Great Lakes Connecting Channels Study, a great deal has been learned about the sources, fate, and effects in the Great Lakes. Two excellent overviews of what we have learned through these and other programs about the sources and impacts of toxic substances in large lakes are presented in the Proceedings of the World Conference on Large Lakes (Schmidtke 1988), held on Mackinac Island, Michigan, in May of 1986, and in a recent report of toxic chemicals in the Great Lakes compiled by three Canadian agencies (Environment Canada, Department of Fisheries and Oceans, and Health and Welfare Canada 1991).

In addition to the impacts of toxic substances on ecosystem and human health in the Great Lakes basin, there are a variety of other issues faced by the stakeholders within the basin. Among these issues are unstable lake levels and coastal erosion; beach closings due to pathogen contamination; eutrophication and hypolimnetic oxygen depletion; urban and agricultural nonpoint source pollution; contaminated sediments; intermedia transfers (e.g. atmospheric deposition); fish stocking practices and conflicts between commercial and recreational fishing interests; preservation of wetlands; and invasion of exotic species (such as the zebra mussel). All of these concerns are inextricably intertwined in such a way that application of a management strategy to address one of them will have ramifications on one or more of the others. In spite of great strides over the last 20 yr in Great Lakes research and management, we have yet to develop sufficient understanding of the behavior of these massive systems to be able to anticipate and account for all of the potential interactions among management strategies.

Recognizing that the implementation of a solution for one resource problem cannot be performed in isolation of others, contemporary Great Lakes managers have generated management concepts and programs that take a more holistic and integrated perspective and emphasize a much broader definition of ecosystem than their predecessors. Some of the environmental management concepts now being applied to the Great Lakes include ecosystem approach, sustainable development, ecosystem objectives, risk assessment methods, toxic mass balance modeling, zero discharge, virtual elimination, pollution prevention, and shared decision-making. Recent programs in the Great Lakes embracing these concepts include Lakewide Management Plans, Remedial Action Plans for Areas of Concern, the Great Lakes Water Quality Initiative, and the Binational Great Lakes Pollution Prevention Strategy. It is axiomatic that all of these concepts and programs can benefit greatly from a synthesis and holistic evaluation of knowledge on the status and functioning of the Great Lakes. The intent of the series of papers that follow is to provide such a synthesis of information on Lake Ontario.

Lake Ontario is a Great Lake which presents an excellent case study for the ecosystem synthesis approach. While it is the smallest of the Great Lakes in surface area (18 960 km^2), it has a larger volume (1640 km^3, because of its 86-m average depth) and longer hydraulic retention time (approximately 8 yr) than Lake Erie. The Lake Ontario drainage basin (64 030 km^2,

largest ratio of drainage basin area to lake surface area of the five Great Lakes) is almost two thirds forest land and approximately 20% agricultural; however, there is considerable urban/industrial development on its shores. Its economic value encompasses all of the areas mentioned above for the Great Lakes. In particular, it supports a significant commercial and sport fishery for both the United States and Canada; major lake trout and salmon stocking programs are ongoing in Lake Ontario. Also, in large part due to its position in the Great Lakes system (furthest downstream and downwind), it has experienced virtually all of ecosystem problems identified above as plaguing the Great Lakes.

Lake Ontario has experienced the significant Great Lakes eutrophication problems of the 1960's and 1970's as well as the recovery through the 1980's resulting from phosphorus management strategies within the basin. This nutrient history has been well documented by such studies as the 1972 International Field Year for the Great Lakes (IFYGL) and the Lake Ontario Nutrient Assessment Study (LONAS) 10 yr later (Lean 1987). Phosphorus enrichment and resulting eutrophication is not the only problem experienced by the Lake Ontario ecosystem, however. Its shoreline residents suffer from the effects of water level fluctuations. It has its share of Great Lakes Areas of Concern that have endured the complete range of impacts common to populated nearshore regions within the basin. But probably most of all, Lake Ontario typifies the current struggle within the Great Lakes with the problem of toxic contaminant (organic chemicals and heavy metals) exposure, bioaccumulation, and ecological and human health effects.

The severity of the toxics problem in Lake Ontario prompted the formation of a Lake Ontario secretariat (comprising four jurisdictional parties: U.S. EPA, Environment Canada, New York State Department of Environmental Conservation, and Ontario Ministry of the Environment), which developed and is continuing to update and implement a Lake Ontario Toxics Management Plan (Lake Ontario Secretariat 1990). This plan draws on studies in the United States and Canada to document the bioaccumulation and effects of such contaminants as PCB's, 2,3,7,8-TCDD, mirex, mercury, DDT and metabolities, hexachlorobenzene, and dieldrin. Because of biomagnification factors for predatory fish as high as 10 million, game fish body burdens have exceeded FDA action limits, prompting fish consumption advisories. There is a growing body of evidence linking cancerous tumors, birth defects, and reproductive failures among large fish and piscivorous wildlife in the watershed to toxic chemical contamination. While the Great Lakes Water Quality Board of the IJC (GLWQB 1987) has noted significant reductions in toxic chemicals in biota of Lake Ontario (specifically in fish and herring gull eggs), these residues have leveled off in the past 5 yr or so. It remains to be seen if the system has reached a new steady state with respect to toxic inputs and, if so, what is the major source driving this observation.

The discussion of problems and management programs in the Lake Ontario ecosystem serves to emphasize the need for a holistic understanding of the functioning of the ecosystem and its response to perturbations. If we are ever to be able to predict the system response to a variety of management programs operating in parallel (e.g. nutrient reduction, fish stocking, nonpoint source reduction, zebra mussel control), we *must* understand and quantify the potential feedback among the various components of the ecosystem. For example, suppose exposure of a certain biotic population to a toxicant has the effect of reducing its reproduction rate. This effect would impact the energy transfer through the food web, which in turn could impact toxicant sorbent (biotic particles such as phytoplankton) concentrations, and ultimately close the loop by affecting exposure. A similar type of feedback sequence of events could result from phosphorus load reductions or the introduction of an exotic species, such as zebra mussels.

The papers in this issue form the basis for development of a new "ecosystem perspective." Each of the authors was asked to (1) attempt a comprehensive overview concerning our present knowledge of Lake Ontario in their respective research area, (2) integrate the socioeconomic and political systems within the basin with the physical, chemical, and biological systems under examination, and (3) identify gaps in information and understanding that pertain to both science and management, in this way drawing attention to key research needs for intelligent and informed policy formulation.

Overview

The 10 papers that comprise this compendium can be categorized as either providing a background description of some aspect of the ecosystem and its interrelationship with the whole system or a discussion of some management issue in Lake Ontario within the context of the authors' own research.

In the first category of papers, a geological perspective of Lake Ontario is presented by Martini and Bowlby (1991). In addition to describing the geologic formation of the basin, the authors point out that there are significant fractures formed by crustal movements, which may serve as pathways for leakage of subsurface contaminants into lake sediments and water column. Regardless of the source of contaminants, interpretation of the relevant chemical and biological processes in the water column requires a thorough understanding of the physical behavior of the lake (water movements, in particular). Boyce et al. (1991) examine our understanding of circulation and mixing in Lake Ontario and the impacts of physical processes on contaminant transport and air–water exchange, relevance of the lake's response to global climate change, and important physical process in bottom sediments (such as sediment focusing).

In the realm of paleolimnology, Schelske (1991) has attempted to use the Lake Ontario sediment diatom, silica, and calcite record to infer the historical dynamics of phosphorus loadings. In addition to presettlement conditions, he has been able to identify the effects of early settlement, the major enrichment from urban sources between around 1940 and the mid-1970's, and the decreased loading due to phosphorus management over the past 15 yr.

Three of the papers deal with a particular biotic community in the Lake Ontario food web. Crowder and Painter (1991) have examined submerged macrophytes in the nearshore regions of the lake. They indicated that macrophyte community stability could be affected by water level fluctuations, sedimentation, wave and ice movement, exotic species invasions, herbivory, eutrophication, turbidity, and contaminants. They observed that recovery has occurred in Irondequoit Bay following phosphorus load reductions. Johannsson et al. (1991) have traced the trends and zooplankton biomass and diversity through the 1980's when phosphorus levels were decreasing and speculated on the factors influencing the changes they observed. Nalepa (1991) has compared the current benthic macroinvertebrate community in Lake Ontario with those of other Great Lakes. He found relatively high oligochaete abundance and a scarcity of pollution-sensitive *Pontoporeia hoyi* in nearshore areas influenced by

municipal and industrial inputs. Noting an almost threefold decline in benthic standing stock in profundal regions, he postulated the cause as an accumulation of toxic contaminants in deep sediments.

Issue-related papers in the series include papers on toxic contamination, nutrient – food web interactions, wetlands, and sport fisheries. Analysis of organochlorine contaminants in spottail shiners by Suns et al. (1991) confirmed the dramatic declines of toxic contamination of Lake Ontario through the late 1970's (69% decline in PCB residues in spottails from 1975 to 1980) as well as the significantly slower declines through the 1980's (17% decline in PCB body burdens of spottails collected at the same sites during 1980–87). PCB and mirex residues in 1987 spottail collections still exceeded IJC aquatic life guidelines at many sites.

The issues related to interactions among various Great Lakes management programs are very complex. Hartig et al. (1991) have addressed the difficult questions surrounding the relative roles of nutrient reduction and salmonid fish stocking in the rehabilitation of Lake Ontario. Using two IJC-sponsored food web dynamics workshops as a basis and observing the response to parallel application of nutrient reduction and food web manipulation in Lake Michigan (both controls combined to enhance water clarity), they speculated on Lake Ontario's response to similar management schemes. They acknowledged that significant uncertainties remain and offered recommendations for research and monitoring that might elucidate the controlling mechanisms. Among their recommendations were (1) the need for various agencies responsible for monitoring various aspects of the ecosystem to coordinate and standardize their efforts and to establish and maintain long-term data sets, (2) the need for controlled, mesoscale experiments to measure process rates necessary to quantify food web interactions, and (3) the need to investigate the impact of changes in food web dynamics on changes in fate and transport of toxic substances in the Great Lakes.

Noting the decline of wetlands in the Great Lakes basin, Glooschenko et al. (1991) reviewed the development over the past 10 yr of Ontario's policy regarding wetland management. They identified the need for a comprehensive program to understand coastal wetlands ecology. In response to this need, they presented an analysis of the patterns of variation in wetland characteristics (wetland type, soils, dissolved solids, vegetation type and diversity) of wetlands along the Ontario coasts of Lakes Huron, St. Clair, Erie, and Ontario.

Finally, Brown et al. (1991) reviewed the socioeconomic research pertaining to the utilization and valuation of Lake Ontario's sport fishery. They discussed the economic impacts of sportfishing on coastal communities, socioeconomic aspects of toxic risk analysis, and communicating risk information to anglers. They also noted research needs in the areas of how toxic contamination and resulting fish advisories have affected the net economic value of sportfishing to anglers and how the public in general responds to information about contaminants in sport fish.

Conclusion

Clearly, the overall health of the Lake Ontario ecosystem has improved over the last decade; however, it is just as clear that it will take many more years to solve the persistent problems that continue to plague the system. Because resources for managing systems such as Lake Ontario are almost always the limiting factor, we must guard against misdirecting those resources to the "wrong problem." Only through a thorough understanding of the structure and functioning of the whole ecosystem can rational, informed decisions be made regarding management priorities. While we certainly have much to learn about the specifics of ecosystem behavior, we desperately need more comprehensive, well-integrated studies such as the Environment Canada LONAS (Lean 1987) and more synthesis documents such as this compendium of papers if we are to truly gain an "ecosystem perspective."

Acknowledgments

I would like to acknowledge Dr. R. Warren Flint for his major contribution to this project. It was Dr. Flint who, some 4 yrs ago, on behalf of the Great Lakes Program at the University at Buffalo, conceived and initiated the "state of the Lake Ontario ecosystem" concept that led to this compendium. The financial support of the Great Lakes Fishery Commission, Ann Arbor, MI, is also gratefully acknowledged.

References

BOYCE, F. M., W. M. SCHERTZER, P. F. HAMBLIN, AND C. R. MURTHY. 1991. Physical behaviour of Lake Ontario with reference to contaminant pathways and climate change. Can. J. Fish. Aquat. Sci. 48: 1517–1528.

BROWN, T. L., B. A. KNUTH, AND F. C. MENZ. 1991. Lake Ontario's sport fisheries: socioeconomic research progress and needs. Can. J. Fish. Aquat. Sci. 48: 1595–1601.

CROWDER, A., AND D. S. PAINTER. 1991. Submerged macrophytes in Lake Ontario: current knowledge, importance, threats to stability, and needed studies. Can. J. Fish. Aquat. Sci. 48: 1539–1545.

ENVIRONMENT CANADA, DEPARTMENT OF FISHERIES AND OCEANS, AND HEALTH AND WELFARE CANADA. 1991. Toxic chemicals in the Great Lakes and associated effects. Vol. I and II. Ottawa, Ont.

GREAT LAKES WATER QUALITY BOARD. 1987. 1987 report on Great Lakes water quality. Report to International Joint Commission, IJC Regional Office, Windsor, Ont. 236 p.

HARTIG, J. H., J. F. KITCHELL, D. SCAVIA, AND S. B. BRANDT. 1991. Rehabilitation of Lake Ontario: the role of nutrient reduction and food web dynamics. Can. J. Fish. Aquat. Sci. 48: 1574–1580.

HERDENDORF, C. E. 1982. Large lakes of the world. J. Great Lakes Res. 8(3): 379–412.

JOHANNSSON, O. E., E. L. MILLS, AND R. O'GORMAN. 1991. Changes in the nearshore and offshore zooplankton communities in Lake Ontario: 1981–88. Can. J. Fish. Aquat. Sci. 48: 1546–1557.

LAKE ONTARIO SECRETARIAT. 1990. Lake Ontario Toxics Management Plan. A report issued jointly by Environment Canada, Ontario MOE, NYSDEC, and U.S. EPA.

LEAN, D. R. S. [ED.] 1987. Studies on the nutrient status of Lake Ontario. Can. J. Fish. Aquat. Sci. 44: 2039–2241.

MARTINI, I. P., AND J. R. BOWLBY. 1991. Geology of the Lake Ontario basin: a review and outlook. Can. J. Fish. Aquat. Sci. 48: 1503–1516.

NALEPA, T. F. 1991. Status and trends of the Lake Ontario macrobenthos. Can. J. Fish. Aquat. Sci. 48: 1558–1567.

SCHELSKE, C. L. 1991. Historical nutrient enrichment of Lake Ontario: paleolimnological evidence. Can. J. Fish. Aquat. Sci. 48: 1529–1538.

SCHMIDTKE, N. W. [ED.] 1988. Toxic contamination in large lakes. Vol. I-IV. Lewis Publishers, Inc., Chelsea, MI.

SMITH, P. G. R., V. GLOOSCHENKO, AND D. A. HAGAN. 1991. Coastal wetlands of three Canadian Great Lakes: inventory, current conservation initiatives, and patterns of variation. Can. J. Fish. Aquat. Sci. 48: 1581–1594.

SUNS, K., G. HITCHIN, AND E. ADAMEK. 1991. Present status and temporal trends of organochlorine contaminants in young-of-the-year spottail shiner (*Notropis hudsonius*) from Lake Ontario. Can. J. Fish. Aquat. Sci. 48: 1568–1573.

Geology of the Lake Ontario Basin: A Review and Outlook

I. Peter Martini

Department of Land Resource Science, University of Guelph, Guelph, Ont. N1G 2W1, Canada

and John R. Bowlby

Geotechnical and Hydraulic Engineering Department, Ontario Hydro, 700 University Avenue, Toronto, Ont. M5G 1X6, Canada

Martini, I. P., and J. R. Bowlby. 1991. Geology of the Lake Ontario basin: a review and outlook. Can. J. Fish. Aquat. Sci. 48: 1503–1516.

Lake Ontario, located at the northern margin of the Appalachian Basin, occupies a deep trough cut by rivers and glaciers into early to mid-Paleozoic limestones and shales. It is still being affected by movements along faults which have probably been active since late Precambrian (more than 600 million yr ago), as evidenced by small faults, "pop-ups" (small domes and anticlines) involving bedrock, Pleistocene drift (glacial and nonglacial deposits) and recent lacustrine sediments, and many small earthquakes (up to intensity V in the Mercalli scale). Infrequent large earthquakes may damage buildings and trigger slumps along coastal bluffs and subaqueous lacustrine slopes. Fractures generated by such crustal movements may become pathways for groundwater and leakage of stored dangerous substances. The lake receives sands from shore erosion of Pleistocene drift and silts and clays from rivers crossing vast Pleistocene lacustrine plains subjected to agricultural practices. Some of the nearshore, subaqueous sand deposits cannot be readily exploited for aggregates because shore erosion may be triggered and valuable ecosystems can be destroyed. Clays mop up pollutants, in part storing them in depocenters such as lagoons, marshes, and the deep lacustrine basins, and in part exporting them to the St. Lawrence River system.

Le lac Ontario, situé à la limite nord du bassin des Appalaches, occupe une auge profonde creusée par des rivières et des glaciers dans des calcaires et des schistes argileux datant de la période s'étendant du début au milieu du Paléozoïque. On y observe encore des mouvements le long de failles probablement actives depuis la fin du Précambrien (il y a plus de 600 millions d'années), comme en témoignent la présence de petites failles, de saillies (petits dômes et anticlinaux) impliquant la roche-mère, de matériaux transportés au Pléistocène (dépôts glaciaires et non glaciaires), de sédiments lacustres récents et l'occurence de nombreux petits tremblements de terre (d'une intensité pouvant atteindre V à l'échelle de Mercalli). De gros tremblements de terre, plus rares, peuvent endommager des édifices et provoquer des glissements de terrain le long des escarpements riverains et des pentes lacustres immergées. Les eaux souterraines et les écoulements de substances dangereuses entreposées peuvent emprunter les fractures générés par ces mouvements de la croûte terrestre. Le lac reçoit des sables provenant de l'érosion de dépôts morainiques du Pléistocène de même que des limons et des argiles charriés par des rivières traversant de vastes plaines agricoles lacustres formées au Pléistocène. L'exploitation de certains dépôts de sable immergés et situés près des rives pour la production d'agglomérats pose problème, car elle pourrait éroder les rives et détruire des écosystèmes importants. Par ailleurs, les argiles absorbent les polluants et les accumulent en certains endroits, comme les lagunes, lar marais et les bassins lacutres profonds, ou les transportent vers le bassin du Saint-Laurent.

Received January 24, 1989
Accepted June 26, 1990
(JA035)

Reçu le 24 janvier 1989
Accepté le 26 juin 1990

Much is known about the general geologic framework of the Lake Ontario region, but several fundamental questions remain. For instance:

(1) Are the location and shape of the lake basins directly or indirectly related to tectonic influences rather than solely to differential erosion by rivers and Pleistocene glaciers? Note that still-active earth movements may endanger buildings and break seals of stores of dangerous substances.

(2) What is the relationship of the underlying geology to the geomorphology of the shoreline? Can erosional sites and nearshore sedimentation sinks (marshes, drowned valleys) be better defined and therefore their development and behaviour be better understood?

(3) What are the primary sources and processes of distribution of Holocene (modern) lacustrine sediments and thus of any attached pollutants? Note, for instance, that about 50% of the fine sediments presently being deposited in Lake Ontario are derived from erosion of the clay-rich drainage basin of Lake Erie.

This paper briefly reviews the general geology of the Lake Ontario region and offers an insight into promising ongoing and future research on the origin and structure of the basin. An improved understanding of dynamic geologic processes which have molded and are still operating within the basin should enhance the development of responsible management of the Lake Ontario ecosystem.

Pre-Quaternary Geology

Lake Ontario is located in a large depression bounded by Paleozoic and Precambrian bedrock highs: to the northwest, the Algonquin Arch; to the south, the Allegheny Plateau (Alle-

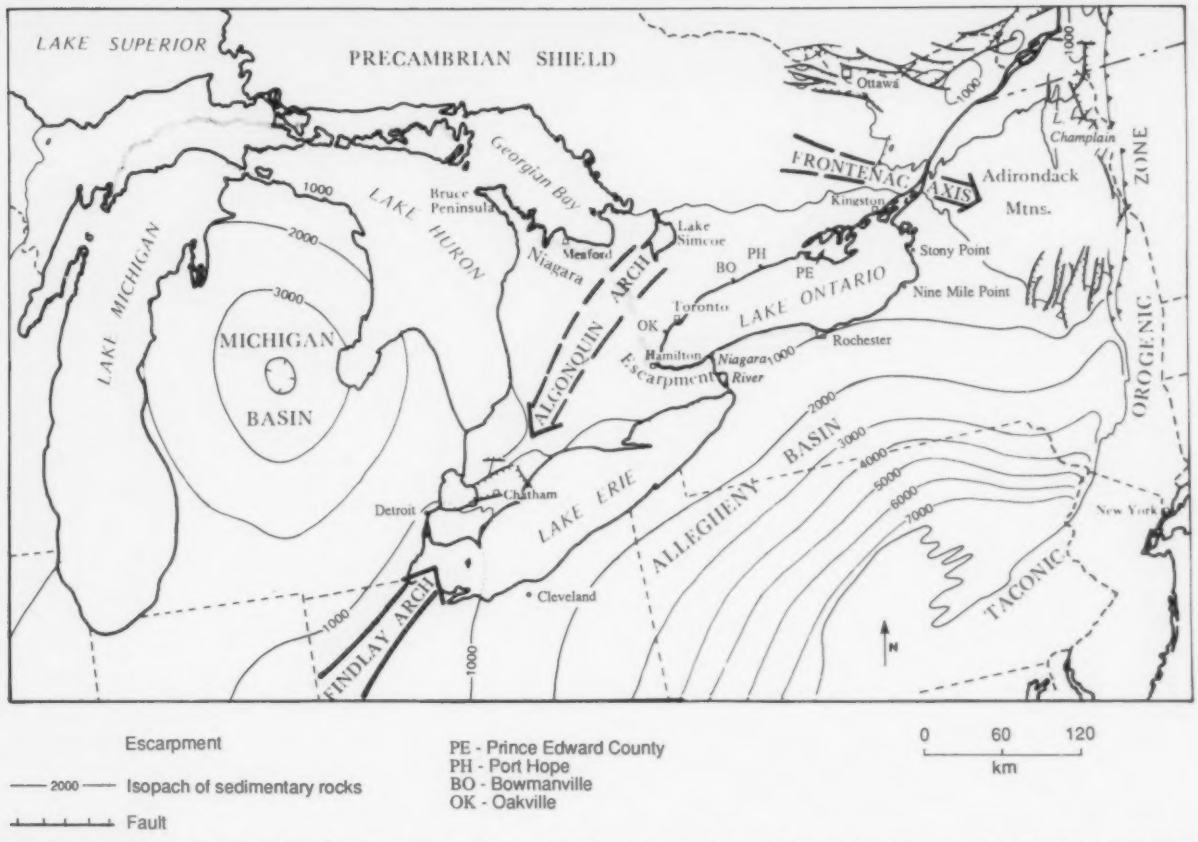


FIG. 1. Geological setting of southern Ontario. Isopachs show total thickness (metres) of post-Precambrian (Phanerozoic) rocks. Lines with barbs indicate faults.

gheny Basin); and to the east, the Precambrian Frontenac Axis and the Adirondack Mountains (Fig. 1).

The basin is underlain by sequences of Paleozoic rocks (Fig. 2): Cambrian to Lower Ordovician sandstones and limestones to the east and in the north central areas, and Upper Ordovician red shales to the west and south (Hough 1958). Resistant carbonate outcrops form an irregular shoreline in areas such as Prince Edward County (peninsula) and much of eastern Lake Ontario, bluffs of red shales occur between Oakville and the Niagara River, and sandstones crop out along the south shore east of Rochester, NY. Pleistocene glacial drift forms most of the remaining shoreline.

The basin is subparallel to the regional strike of southeasterly dipping bedrock units (Hough 1958). A north–south cross-section through Lake Ontario and Lake Erie indicates that both lake basins have been eroded into Paleozoic shales and bounded by escarpments (cuestas) composed of more resistant carbonates and sandstones (Fig. 3).

Since mid-Paleozoic times, much of the region has been exposed and considerable erosion has occurred. In situ petroleum in interreefal Silurian rocks (Eramosa Formation) suggests that the Paleozoic rocks presently occurring in southern Ontario may have been buried under 2000–3000 m of other sedimentary rocks (possibly late Paleozoic or/and Mesozoic (?) rocks), that is, to depths at which the temperature was sufficiently high for transformation of organic matter into hydrocarbons to occur. These overburdened rocks have been eroded by rivers and glaciers. The rivers established an extensive drainage system, part of which may have flowed eastward into a pre-Pleistocene proto-St. Lawrence River, the "Laurentian River" (Spencer 1890), and part southwestward into the Mississippi River system. The river valleys which cut deeply into the more erodible shales formed the precursors to the lower Great Lakes.

Quaternary Geology

During the Pleistocene (glacial) and Holocene (postglacial) times, a complex record of erosion and deposition developed in the Lake Ontario basin. During glaciation, the continental ice sheets flowed from the north and northeast and when they reached the Great Lakes region were funnelled, thickened, and moved as lobes into the preexisting river valleys (Prest 1970; Gadd 1980; Muller and Prest 1985). Local focussing and ice thickening increased the erosional power of the glaciers, and the valleys were deepened, widened, and changed into broad depressions (Fig. 4A). Because subsequent glaciers reworked preexisting material, the best preserved and understood record is that of the last glaciation and succeeding deglaciation. Well-known examples of moraines, till plains, drumlins, eskers, and subaerial and subaqueous outwash occur near and at the lake shore (Fig. 5) (Coleman 1936; Karrow 1967; Singer 1974; Brookfield et al. 1982; Chapman and Putnam 1984; Sly and Prior 1984).

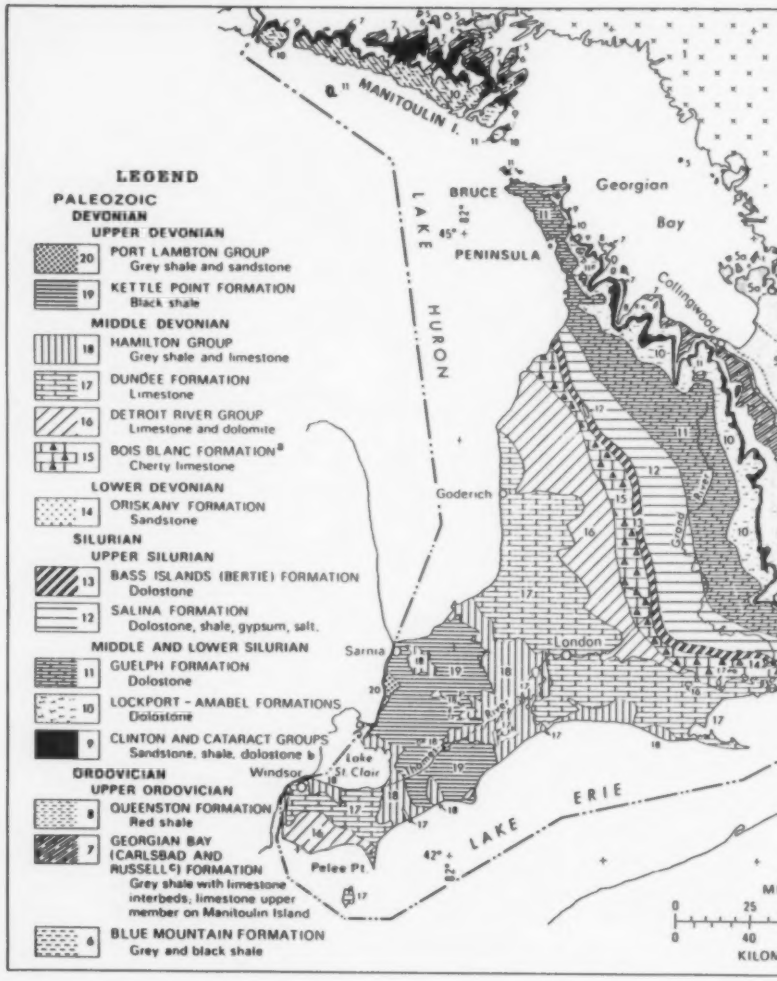
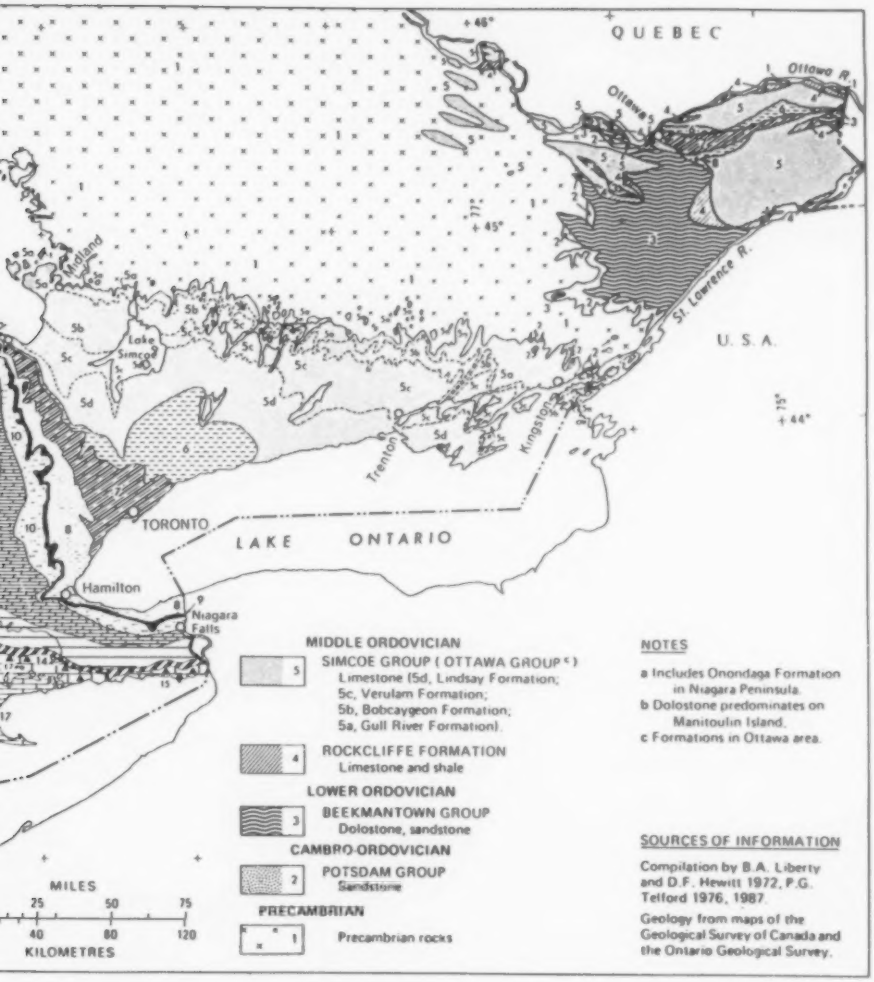


FIG. 2. Geologic map and stratigraphic units of southern Ontario (compiled by the Ministry
Geological Survey and the Geological Survey of Canada).



linistry of Northern Development and Mines, Ontario, from published and unpublished maps of the Ontario

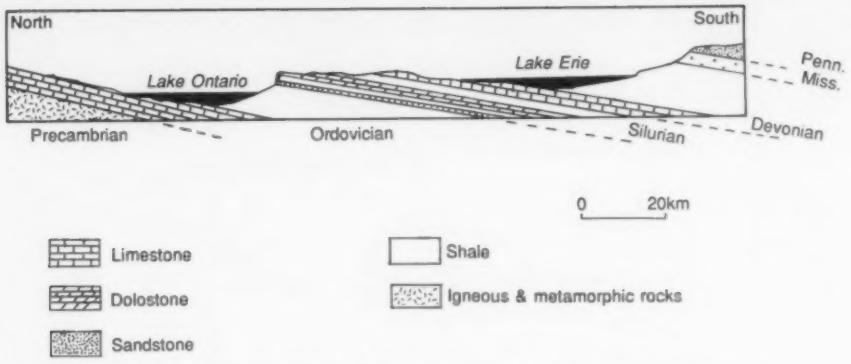


FIG. 3. Geologic cross-section of Lake Ontario and Lake Erie (from Hough 1958).

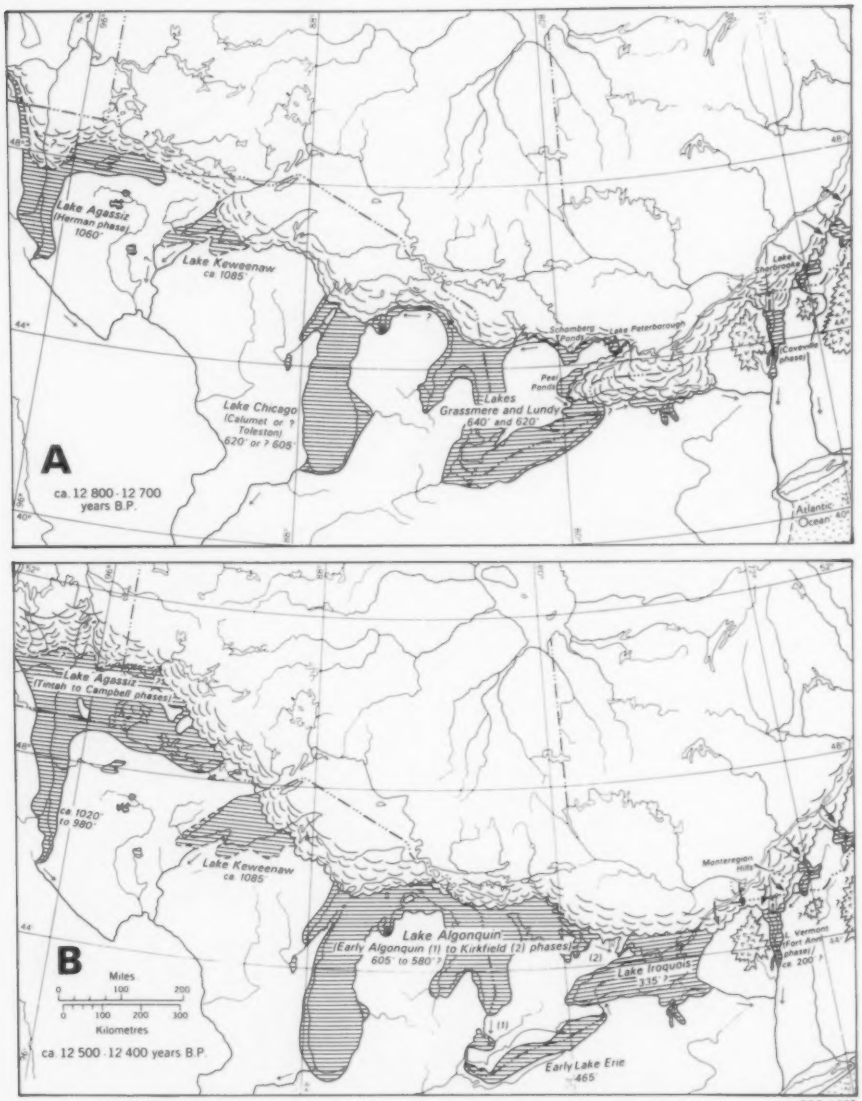

Lake Agassiz (Herman phase) 1060'
Lake Keweenaw ca. 1085'
Lake Chicago (Calumet or ? Toleston) 620' or ? 605'
Lakes Grassmere and Lundy 640' and 620'
Schomberg
Peterborough
Pefferlaw
Cavendish phase)
Atlantic Ocean
A
ca. 12 800 - 12 700 years B.P.
Lake Agassiz (Tintah to Campbell phases)
ca. 1020' to 980'
Lake Keweenaw ca. 1085'
Lake Algonquin (Early Algonquin (1) to Kirkfield (2) phases) 605' to 580'
Lake Iroquois 315' ?
Early Lake Erie 465'
Monteregian Hills
Vermont (Fort Ann phase) ca. 200' ?
B
Miles
Kilometres
ca. 12 500 - 12 400 years B.P.
GSC 1967

FIG. 4. Glacial maps showing edge of glaciers and extent of early stages of the Great Lakes. (A) 12 800 yr B.P.; (B) 12 500 yr B.P. (from Prest 1970).

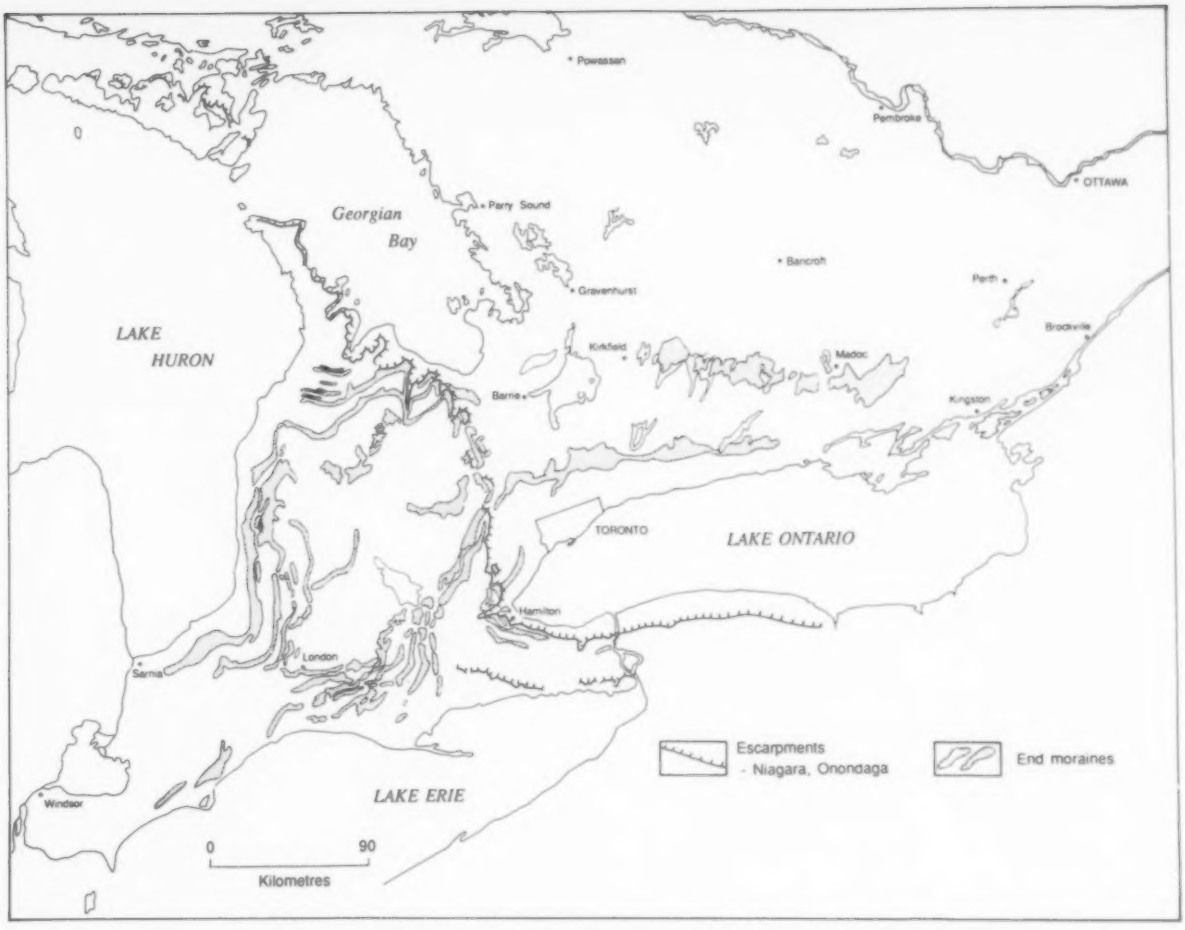


FIG. 5. Generalized Pleistocene map of southern Ontario showing distribution of end moraines (Chapman and Putnam 1984).

During the early stages of last deglaciation of southern Ontario, large proglacial lakes (with at least one side bounded by the glacier) developed. Considerable quantities of silt and clay were deposited, for instance, across southwestern Ontario, and large sandy deltas formed in some areas (Chapman and Putnam 1984; Kelly and Martini 1986).

As deglaciation continued, the glacial lobe covering the Lake Ontario basin melted and a wide, deep, high-level Lake Iroquois developed while the present St. Lawrence outlet was still dammed by ice (Fig. 4B). Progressively lower outlets were uncovered from the ice, and lake levels dropped to a low postglacial stage betwen 11 700 and 11 400 yr ago (Sly and Prior 1984). This low lake level is termed the Admiralty phase of early Lake Ontario and marks the opening of drainage (due to melt out of the glacier barrier) through the isostatically lowered St. Lawrence valley (Sly and Thomas 1974; Bowlby 1975; Sly and Prior 1984; Anderson and Lewis 1985). Subsequent isostatic rebound around the Lake Ontario basin has been greater to the northeast than to the southwest, raising the outlet still near Kingston. This differential uplift of the land led to postglacial lake levels rising differentially to the southwest; the temporary high water peak of about 4000 yr B.P. marks the transfer of Upper Great Lakes (Lake Huron and Lake Superior) drainage through Lake Erie and Lake Ontario (Fig. 6) (Anderson and Lewis 1985). A linear rate of naturally increasing elevation of the water plane in western Lake Ontario (Port Dalhousie) has been determined as 2 mm/yr based on recorded water level data since 1860 (Price 1954; Clark and Persoage 1970).

Considerable information about the Quarternary sediments of the basin is available (Sutton et al. 1970; Lewis and Sly 1971; Sutton and Woodrow 1972; Thomas et al. 1972a, 1972b; Sly 1977, 1983a, 1983b, 1984, 1986; Sly and Lewis 1972; Sly and Prior 1984; Rukavina 1976). However, improved mapping and understanding of the Pleistocene sequences exposed along the coastal bluffs are required because they constitute one of the source areas for modern sediments of the lake. For instance, in the Toronto–Scarborough area, a large amount of silty and sandy deltaic sediment occurs. Farther to the east in the Bowmanville – Port Hope area, more variable material is present ranging from bouldery till to gravel, sand, and silt (Gadd 1980; Brookfield et al. 1982; Martini et al. 1984; Kelly and Martini 1986).

Little published information is available on the thick Pleistocene sequences in the deeper parts of the lake (Lewis and Sly 1971; Anderson and Lewis 1975). Although shallow surface sediment coring and nearshore sediment description programs have been undertaken, no systematic drilling study has been made of the lake bottom. Side-scan sonar, seismic, and acoustic

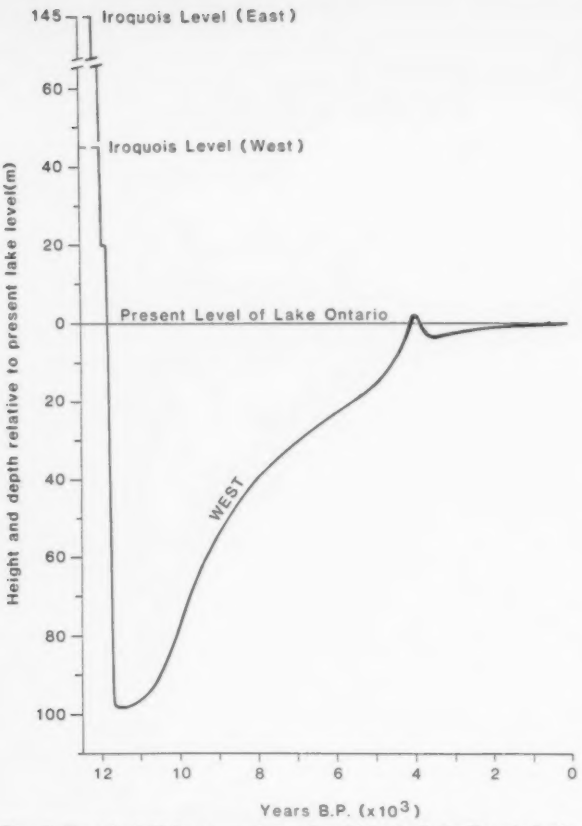


FIG. 6. Postglacial lake stages (water levels) in the Lake Ontario basin (modified from Anderson and Lewis 1985).

profiles have been used to establish the general stratigraphy in some parts of the lake, but lakewide correlations have not been established (Sly and Prior 1984). The deep portions of the basin are expected to contain valuable stratigraphic information. This should record the transition from an erosional stage during the maximum glaciation when the glacier ice was several kilometres thick and was grounding throughout the basin to a depositional stage when the receding, thinning glacier must have been floating at some time during the melting period. The sedimentary record may not be thick and it may be patchy, if the rate of melting of the glacier was rapid, but that area is likely to contain the most complete record of glaciation in the Great Lakes region.

These data are of particular importance in understanding not only paleoclimatic conditions and events, but also as the basis for models of glacial and postglacial seismic and tectonic activities in the region.

Geomorphology and Sedimentation

The coast is indented by several drowned valleys (river valleys submerged during the postglacial lake level rise) which constitute sediment and thus also pollutant traps (Otto and Dalrymple 1983). Numerous coastal lagoons and marshes also constitute sediment depocenters for discharging streams or for lacustrine storms and form productive habitats for wildlife, primarily migratory birds.

Longitudinally, Lake Ontario has been subdivided into three deep sedimentary basins, the Niagara, Mississauga, and Rochester basins, separated by bathymetric sills, and a fourth shallow (less than 40 m deep) basin, the Kingston basin, situated at the eastern end of the lake (Fig. 7A; Thomas et al. 1972a, 1972b). The deepest part of the Lake Ontario basin (depth about 242 m) is in the central portion of the Rochester Basin. The easternmost sill, the Duck-Galoo Sill, is a subaqueous escarpment of Paleozoic rocks which trends easterly from Prince Edward County, Ontario, towards Stony Point, New York. The deeper Whitby–Olcott and the Scotch Bonnet sills were thought to be Pleistocene depositional features, but the Scotch Bonnet sill, at least, is now found to be a bedrock feature (Anderson and Lewis 1975).

Modern lake sediments are distributed following an energy gradient from nearshore gravels and sands to deepwater silt and clay (Sly 1980). For instance, Sly (1983b) reported that "off the Niagara River mouth, rates of accumulation of sandy silts (at about 30 m depth) are about 1.8 mm/year, clayey silts (at depths between 70 and 90 m) range between 1.4 and 0.2 mm/year, and silty clays (more than 100 m depth) are about 0.08 mm/year."

The sandy materials of the lake are derived from relict Pleistocene to Early Holocene deposits located on the present shelf of the lake, or from coastal bluffs (Environment Canada 1975; Haras and Tsui 1976). Little sand is being introduced by rivers (Kemp and Harper 1976; Ongley et al. 1977). The sand is actively redistributed by nearshore drift processes and moves shoreward under the influence of strong waves and winds at selected locations in the lake (Fig. 7B) (Rukavina 1976; Owens 1979). High wave conditions which occur both at the eastern and western ends of the lake rework bottom sediments to depths greater than 20 m, as evidenced by sedimentary structures in sand and by lag deposits.

In deeper parts of the subbasins, there are relatively high rates of fine-particle sedimentation, with a maximum of 2.59 million metric tons per year in the Rochester Basin (Kemp and Harper 1976). It is interesting to compare the rates of sedimentation with rates of input and output of fine sediments (Fig. 7B). Relatively little fine sediment is derived from shore erosion (from tills and clay rich rhytmites); most is derived from river inputs, and 50% of the total input comes from the Niagara River. This is not surprising, as most of the fine material derives from erosion of the lacustrine clay plains of the eastern part of the Lake Erie basin which are subjected to intense agriculture practices (Fig. 5) (Prest 1970; Wall et al. 1982). About one third of the fine material contributed to Lake Ontario is removed through the St. Lawrence outlet, some settles in coastal lagoons and marshes, and the rest is deposited in the deep sedimentary basins. A corollary to this is that ions, including toxic pollutants, which attach to fine sediment particles in Windsor, Detroit, Cleveland, and other localities in Lake Erie or along the Niagara River, may subsequently affect inhabitants of Rochester and Toronto in Lake Ontario and even the inhabitants of Montreal and Quebec City along the St. Lawrence River.

The amount of information about modern sediments in the lake is large, and inventories of their ages, rates of sedimentation, and concentrations of many ions have been established (Thomas et al. 1972a, 1972b). Similarly the sources of the sediments and the processes of their dispersal are reasonably well known (Haras and Tsui 1976; Rukavina 1976; Martini and Kwong 1985). At the present, much emphasis is being placed

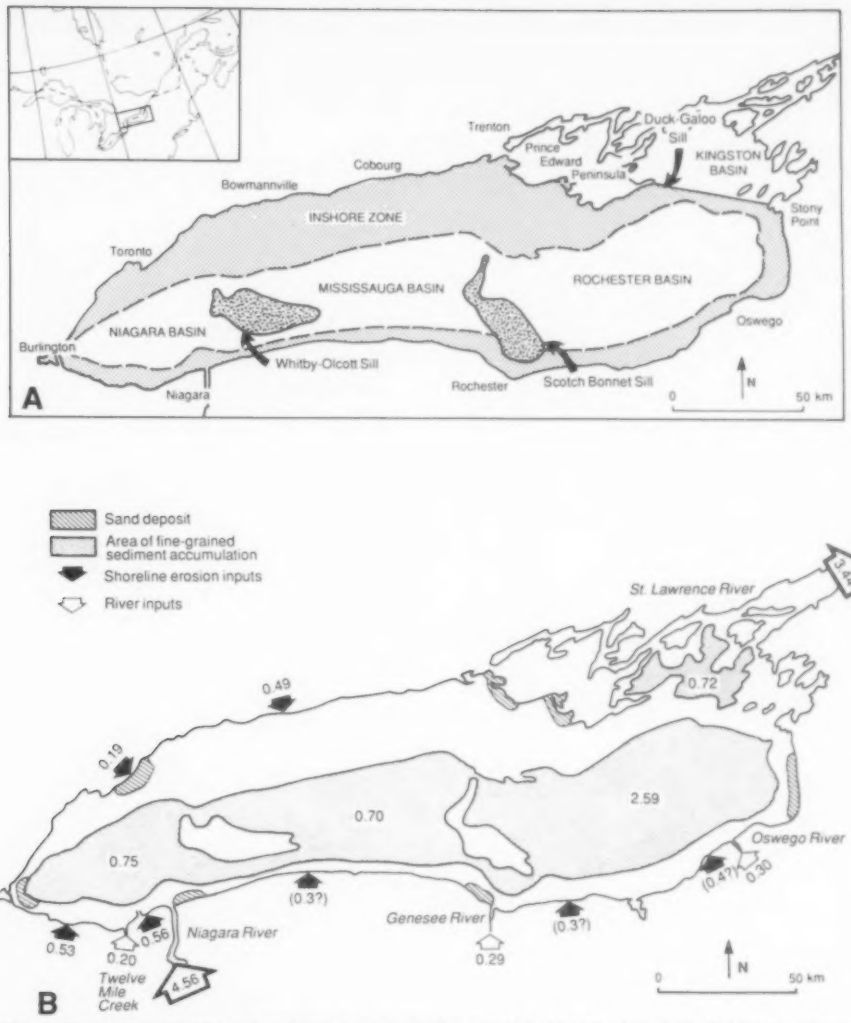


FIG. 7. Depositional subbasins and recent rates of sedimentation. (A) physiography; (B) rates of input and sedimentation of fines (modified from Kemp and Harper 1976).

on the study of the water–sediment interface and on the processes and products of early diagenesis.

Indeed, much is known about the Lake Ontario basin, but it is foolhardy for the population which surrounds the lake and is dependent on it to be complacent or not to demand that such knowledge is used in the development of management plans of the ecosystem. For instance, it is well known that longshore drift is the principal process responsible for the redistribution and accumulation of nearshore sand. A strong drift flows eastward along the south shore toward Rochester from the Niagara River; easterly and westerly drifts occur along the north shore to the east of Toronto. In some locations, the direction of drift changes during storms. Longshore drift is a powerful process which can move much material and create sedimentation problems for industries utilizing nearshore waters for commercial purposes. However, long-range longshore drift may not be the only explanation for all the coastal sand deposits. For instance, in Prince Edward County, drumlins extend from the now-emerged land into the shallow shelf (Leyland and Mihychuk 1984). Associated with them are ancient channels filled with glacial sands (Martini and Kwong 1985). There is evidence that some of the nearshore sands have been derived from these Pleistocene materials and have been reworked shoreward during the rise of lake levels which followed the low stage of the Admiralty phase. At the present high lake stages, these relict subaqueous glacial sands are not readily available for reworking, and the nearshore sand deposits cannot be rapidly replenished by long-range (from distant coastal bluffs) longshore currents. Consequently, their exploitation for aggregates would severely affect the adjacent coasts with which the nearshore sand bodies are now approaching equilibrium.

On the whole, little is known about the effect of the changing lake levels on the sediment distributions. Even less is known about the processes responsible for the inshore–offshore distribution of sediment in the lake. Studies of suspended contaminant tracers which have inshore point sources show complex patterns and timings of dispersal, hence of suspension and solution residence time (most dangerous stage) in the lake (Sly

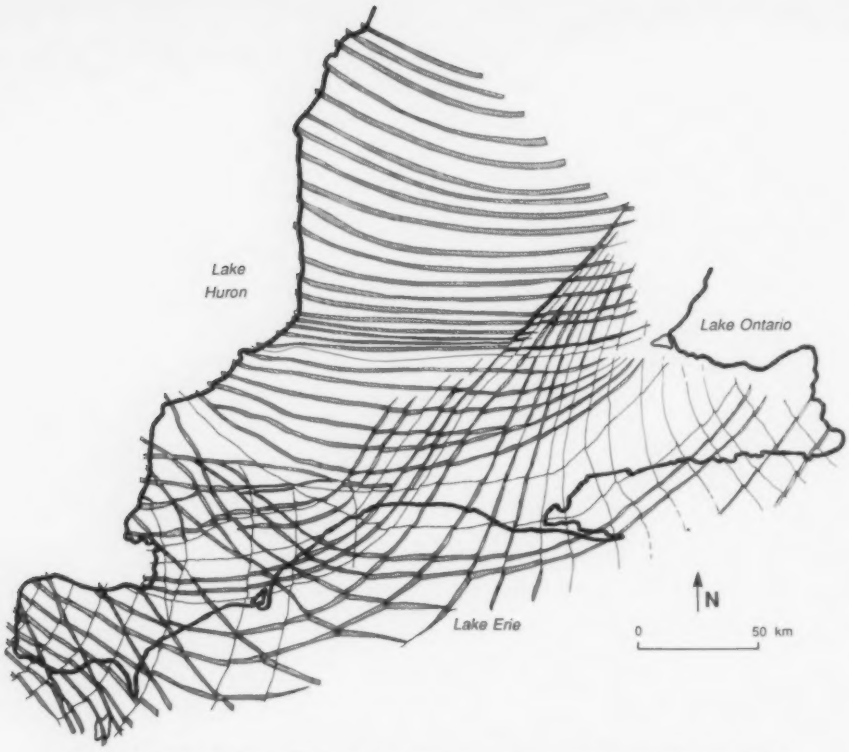


FIG. 8. Subsurface structural trends in southwestern Ontario (after Sanford et al. 1985).

1983a; Thomas and Sly 1988). The understanding of how the offshore distribution occurs in large lakes is critical because lacustrine processes cannot be compared directly with those better studied ones occurring in the marine environment: they differ primarily because of scale, salinity, thermal conditions of the water column, tidal influence, and so on (Sly 1980).

Structure and Tectonics

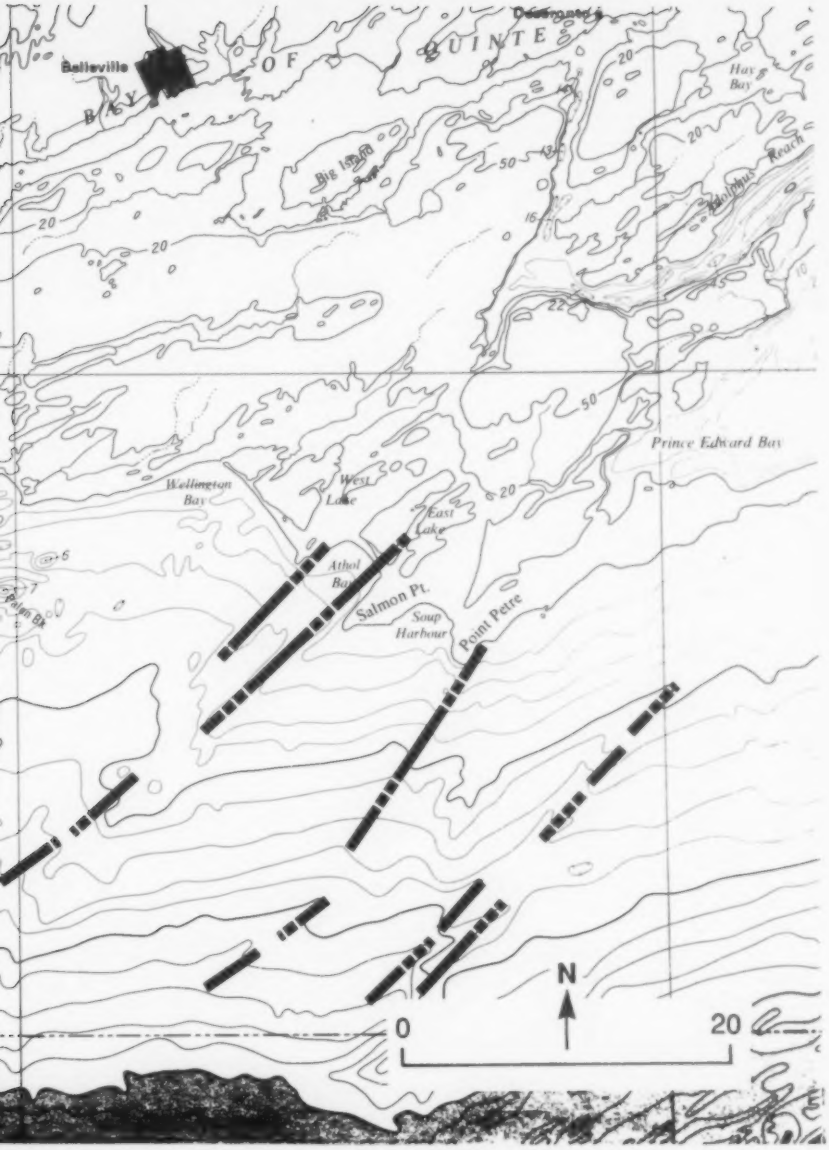
Over the past decade, significant new knowledge has been gained about the structure and tectonics of the Lake Ontario basin and the Great Lakes region as a whole.

The Lake Erie – Lake Ontario – St. Lawrence River valley alignment follows the front of the Taconic orogenic zone and that of the Allegheny Plateau, along the northwest uplifted margin of the Appalachian Basin. There are numerous normal faults along this trend (Fig. 1). They are observed in many locations along the St. Lawrence River, rimming the Ottawa rift valley, they characterize the secondary rifts on the south flank of the Adirondack Mountains, and are also found north of Lake Erie in the subsurface "Chatham sag" (Fig. 1). Furthermore, Sanford et al. (1985) have presented evidence for intense fracturing in Paleozoic rocks of southwestern Ontario and have proposed a conceptual structural model which, to the west of Lake Ontario, is characterized by two intersecting major arcuate fracture trends. One set is aligned east–west and the second southwest–northeast (Fig. 8). Such subsurface structures are thought to have been responsible for the formation of hydrocarbon traps in the area. To the north and east of Lake Ontario, structural alignments are readily observed on satellite imagery, both on the rugged Precambrian terrain and on the Paleozoic rocks (Lowman et al. 1987; Singhroy 1988). These surficial expresions can be mapped to the lakeshore in Prince Edward County where the Paleozoic bedrock is only sparsely covered by Pleistocene sediments (Liberty 1960).

Faultings occur all around the lake and it is only logical that faults must also exist under the lake itself, but where and what kinds of faults are present, and are they active or not? Surficial fault traces of Prince Edward County can be extended into the lake basin along alignments indicated by gravity and aeromagnetic anomalies and by bathymetric contours (Fig. 9) (Canadian Hydrographic Service 1970). Some of these alignments merge with the Scotch Bonnet Sill and then emerge in New York State along the seismically active Clarendon–Linden fault system (Fakundiny et al. 1978; Muller and Prest 1985). In the deep Rochester Basin, numerous local trends are subparallel to the major ones. Their origin, as well as the true nature of the deep sills which subdivide the lake floor, is not well known. However, in 1975, seismic and echo sounder profile lines across the Scotch Bonnet Sill were published showing strong reflectors with a bedrock dislocation approaching 20 m at the sill (Fig. 10) (Anderson and Lewis 1975). At the sill, the bedrock is mantled by a thin, dense Pleistocene material and a very thin lacustrine lag cover. The subaqueous trend of the sill is therefore thought to be controlled by still-active faults.

Additional information about the structural trends is being gathered, collated, and reanalyzed and should provide information on the type and age of the faults (Alexander 1988; Bowlby et al. 1988a, 1988b, 1988c). Recently published maps show strong magnetic anomalies trending across the lake

FIG. 9. Bathymetric map of part of Lake Ontario with a few



ith a few of the major structural alignments (broken lines).

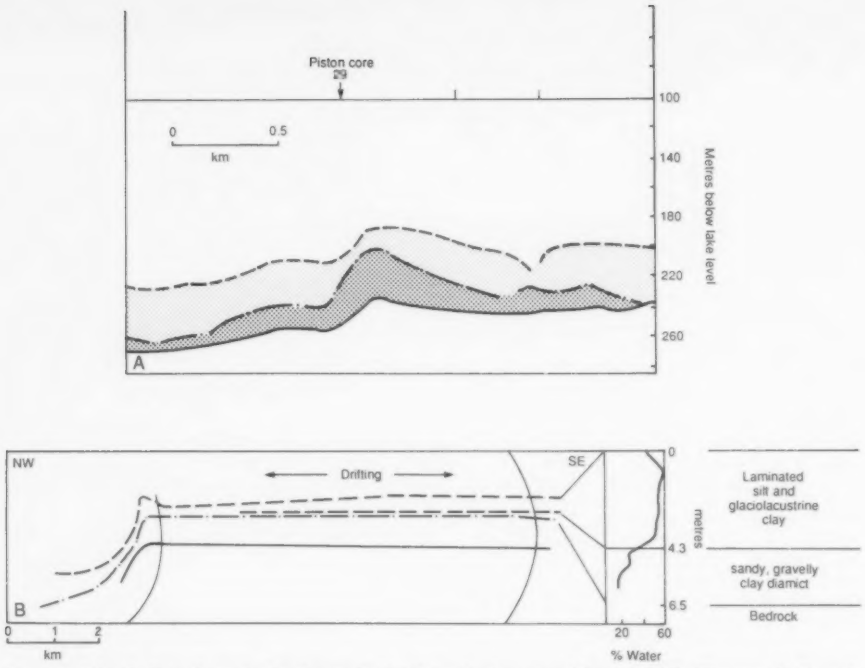


FIG. 10. Seismic lines from the Rochester Basin (from Anderson and Lewis 1975). The zone indicated as "drifting" may have a different scale from the rest of the figure, as the ship was drifting slightly during recording of the data.

(Fig. 11) (Maps 7333G and 7334G, Geophysics Division, Geological Survey of Canada 1987). The trends of the magnetic anomalies are generally subparallel to the structural trends previously noted. They also exhibit similar orientations with low relief features which have been identified in the recent lacustrine sediments by echo sounding and side-scan sonar (Bowlby et al. 1988a; Thomas et al. 1989). Furthermore, minor structural features such as surface "pop-ups" which affect both the Paleozoic bedrock and the mantle of recent sediments have been mapped by the Ontario Geological Survey in Prince Edward County and in other parts of southern Ontario (McFall and White 1987; McFall et al. 1988, 1989). In New York State, large excavations were dug for the cooling towers at the Nine Mile Point Nuclear Power Generating Station and several fractures were exposed (Fig. 12) (Coates 1981). Those fractures cut through the Paleozoic Oswego sandstone, the Pleistocene deposits, and the overlying postglacial lacustrine sediments. Other possible structural evidence of neotectonic (recent tectonic) activity in the Great Lakes region may not have been recognized as such. For instance, numerous folds and faults have been mapped in Pleistocene deposits, and invariably they are interpreted with causal relationships to the melting of buried ice blocks (McDonald and Shilts 1975; Kaszycki 1987). Many indeed may have such origins. However, others that are found along the alignments of bedrock faults and geophysical anomalies may represent the surficial expression of heretofore unrecognized neotectonic movements. Finally, numerous micro-earthquakes, with a few reaching intensity V on the Mercalli scale, occur along the St. Lawrence River and Ottawa valleys. Fewer, but nonetheless relatively large, seismic events have occurred around and within the shorelines of Lake Ontario, Lake Erie, and the adjacent region (Fig. 13) (Chandler and Morey 1988; Green et al. 1987; Quittmeyer et al. 1988).

The parallelism and colinearity of observed bedrock structures and magnetic field anomalies in the Lake Ontario basin suggest that the anomalies represent rocks of different magnetic susceptibilities in the earth's crust. These rocks and features (dikes, faults) were most probably formed during Precambrian time, and the faults have been reactivated throughout geologic time: firstly during the Paleozoic when the area was subjected to stresses associated with the orogeny of the Appalachian Mountains, and subsequently by the unloading due to erosion of sediments during the Mesozoic and the Cenozoic. During the Quaternary era, the same zones of crustal weakness were most probably reactivated again, under the influence of the repeated cycles of supracrustal glacial ice loading and unloading.

The distribution and alignment of the faults and the continuity of earthquake events suggest that the structures of the Lake Ontario and Lake Erie basins represent a westward, midcontinent extension of the St. Lawrence Valley fracture system (Kumarapeli and Saull 1966). Furthermore, it is of interest to note that the junction of the St. Lawrence, Ottawa, and Lake Champlain valleys most probably represents a triple junction point (typical fracture pattern of the earth's crust subjected to a rising hot plume from the underlying mantle), proximal to which are the postorogenic igneous intrusions of the Monteregian Hills, just east of Montreal (Sanford et al. 1985). Recognition of this type of alignment on the continental plate is not unique to the St. Lawrence – Lake Ontario region (Kumarapeli and Saull 1966; Kumarapeli 1987; Cambray 1987, 1988; Hinze et al. 1988; Parrish 1988). Similar trends occur in southeastern Canada and the adjacent United States, and all exhibit a general parallelism to each other (Fig. 14). The axial trend of Lake Superior, for instance, is aligned with magnetic anomalies and

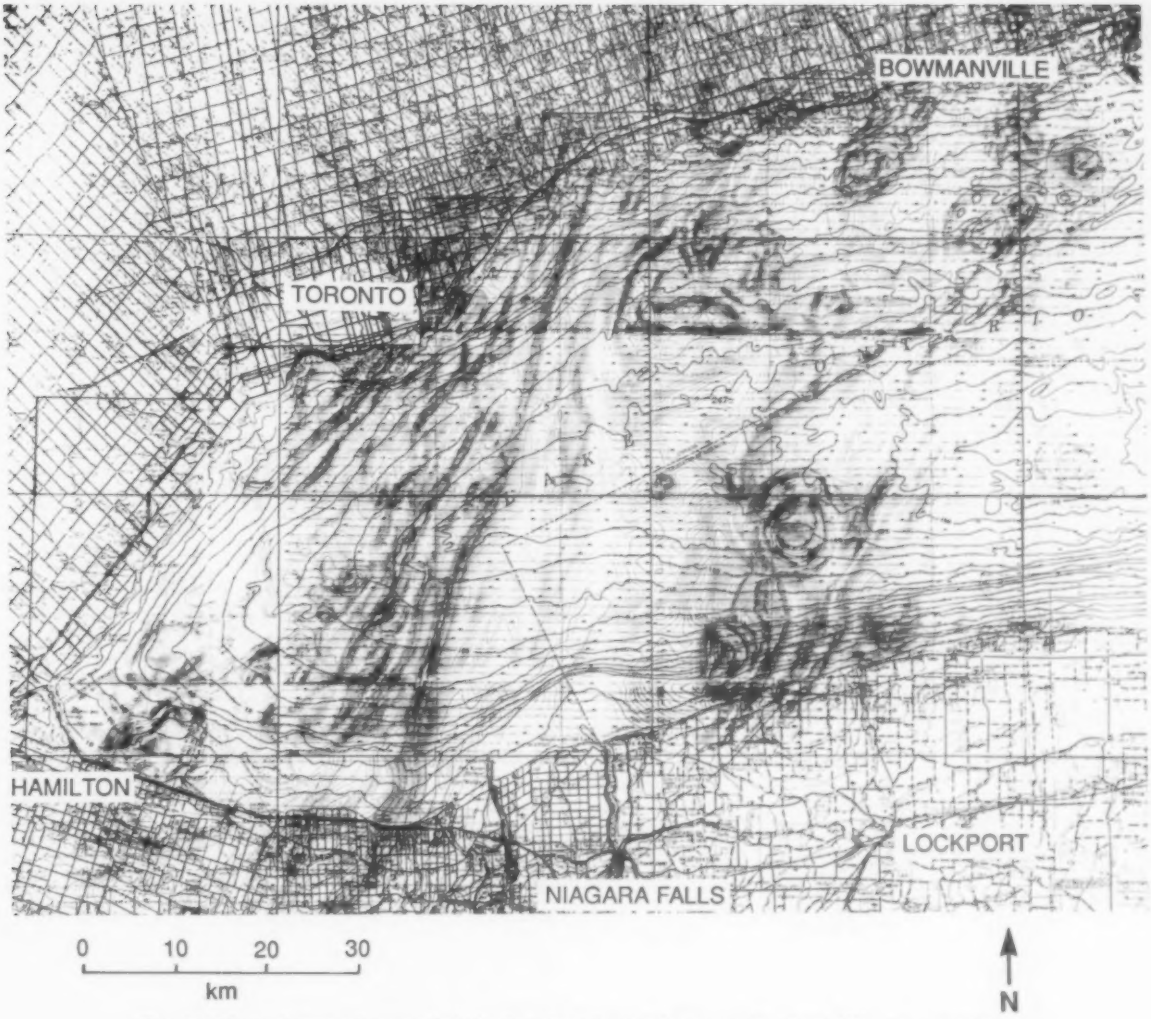


FIG. 11. Magnetic anomalies map in Lake Ontario indicating deep-seated rocks of different composition.

is probably related to a 1 billion yr old rift. A younger trend along the eastern seaboard has been associated with Triassic rifts formed during the early stages of splitting of Pangea (the Late Paleozoic supercontinent), just before the opening of the Atlantic Ocean. The structural trend along the St. Lawrence River and Lake Ontario was formed in a zone marginal to a major orogenic belt. This, as well as the other trends, retains the record of such mountain building (orogenic) episodes even after the land has become tectonic quiescent.

Several questions remain partially unanswered. One question relates to the type of faults present in the Lake Ontario basin, where there is abundant evidence of both normal and reverse (thrust) faulting, thus suggesting that strike-slip (lateral) movements may also be observed in the region. Probable strike-slip movements have been suggested by recent earthquake focal mechanisms which exhibit north–northeast trending strike-slip planes (Quittmeyer et al. 1988). It is not yet known, also, whether the structural alignment directly affected the localization of the lake or had indirect effects in weakening the crust and thereby allowing increased deep weathering and, for instance, fostering karst dissolution of the carbonate bedrock. Most likely the tectonic structures have controlled the location of the lake basin and, together with the differential fluvial and glacial erosion of the bedrock, have contributed to the overall shape including its longitudinal separation into subbasins.

Conclusions

This brief review suggests that location of the Lake Ontario Basin is, in part, controlled by tectonic events and faults and that tectonic activities have continued to affect the basin since Precambrian times; they have influenced the evolution of the lake itself throughout its history to the present day.

Throughout the Pleistocene, the Lake Ontario basin has undergone several episodes of glaciation and deglaciation, with associated sedimentation and erosion similar to that of the other Great Lakes of North America. Most of the inshore and nearshore Pleistocene sediments belong to the Wisconsinian (ultimate) glaciation, with only locally thin remnant deposits of the Illinoian (penultimate) glaciation preserved. Whether or not the glaciers within the lake basin were grounded everywhere at all times or were water supported in some sectors of the lake is

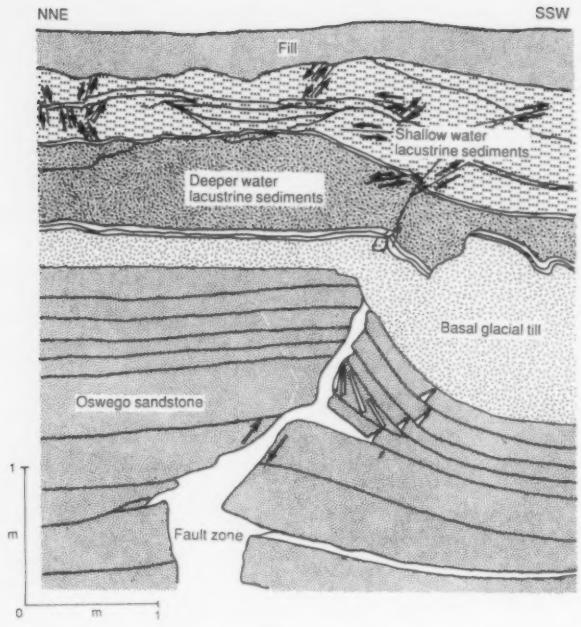


FIG. 12. Diagrammatic section of a pit dug at Nine Mile Point, New York, showing various fractures and faults cutting across Paleozoic and recent sediments (from Coates 1981).

not known. Deep coring, boring, and more extensive acoustic and reflection seismic data are required to define the lakewide distribution of Pleistocene deposits and their stratigraphic continuity.

Although much is known about the modern sediments of the lake, dynamic processes such as the effect of changing lake level on the distribution and redistribution of nearshore sediments and the processes linking nearshore and offshore sediment dispersal are not yet well understood. Similarly, the history of the formation of and the processes of deposition in sedimentary sinks such as the nearshore marshes and drowned valleys are not yet well defined.

The Lake Ontario drainage basin has undergone a population explosion in the past 50 yr and the concentration of people will likely continue to increase into the foreseeable future. Ultimately, an improved analysis of the geology of the region can lead not only to a better understanding of seemingly academic problems such as those of intracratonic tectonics, but also to improved resolution of applied ecological and environmental problems such as the sources of and distributions of sediments and pollutants, both in the main lake itself and in nearshore sediment sinks. New approaches to the understanding of the geologic conditions and for the reduction of uncertainties in the assumptions necessarily made in modelling are required for the evaluation of all facets (that is, seismic, coastal, erosional, and water quality management) in societal risk analyses.

Acknowledgements

We wish to thank the editor, P. G. Sly, and an anonymous reviewer for their help in improving the manuscript. Numerous discussions with

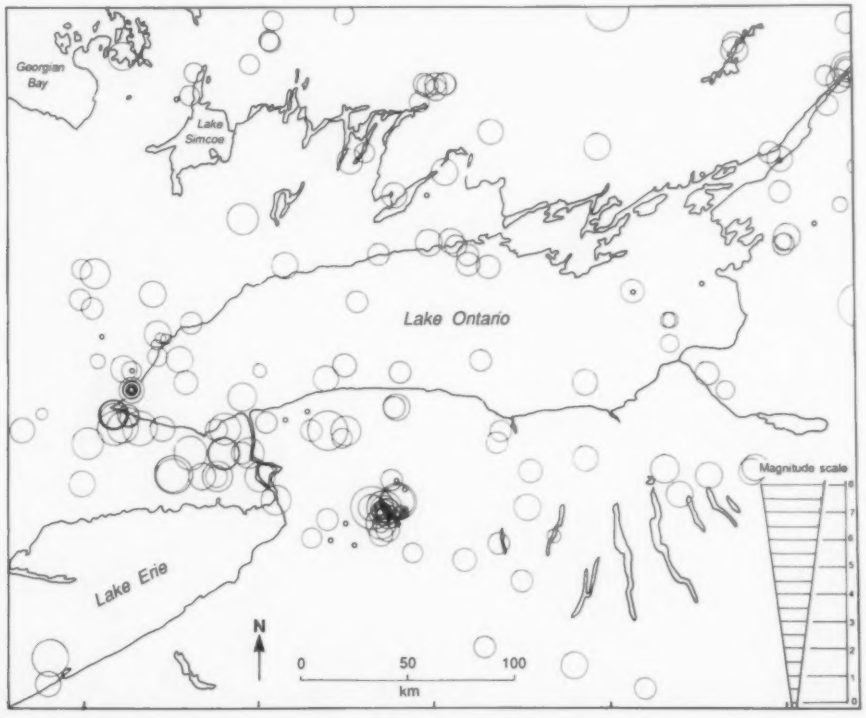


FIG. 13. Seismic records in the Lake Ontario Basin. The diameter of the circles indicates the magnitude of the earthquakes as can be read from the magnitude scale.

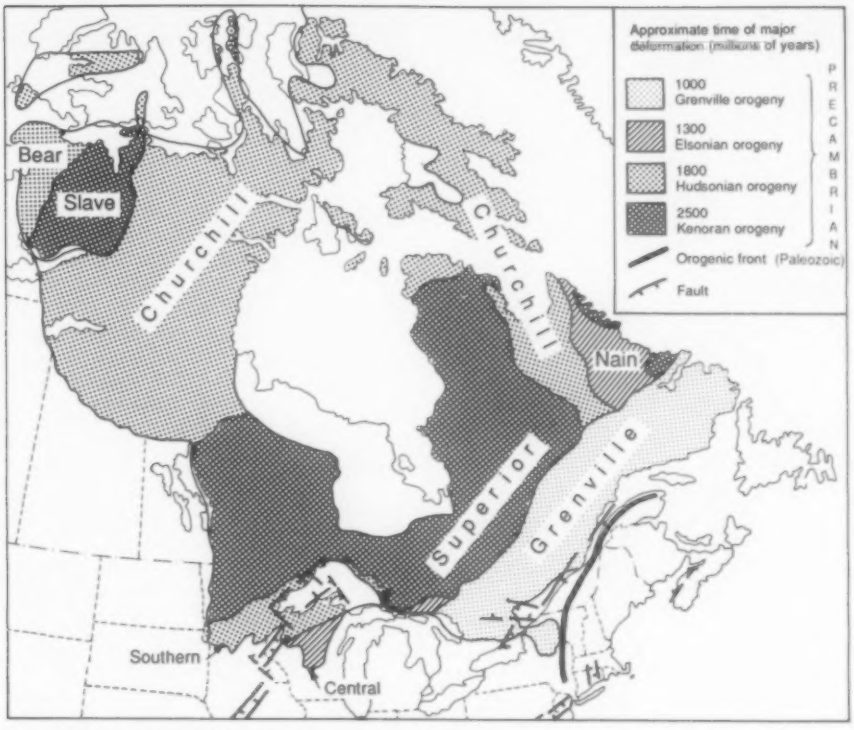


FIG. 14. Precambrian shield of North America with superimposed selected structural trends, indicated by the fault trends (barbed lines) and orogenic (mountain) front.

colleagues in the Great Lakes research community are valued and have helped us to develop some of these concepts. However, the authors are responsible for the opinions which have been expressed herein. Financial support was provided by the Natural Sciences and Engineering Research Council of Canada grant A7371 (to I.P.M.) and by Ontario Hydro (to J.R.B.).

References

ALEXANDER, S. 1988. A seismo-tectonic framework for assessing hazard in the Great Lakes Region. Abstracts with program, 22nd annual meeting, North-Central section of Geol. Soc. Am., Akron, OH. p. 331.

ANDERSON, T. W., AND C. F. M. LEWIS. 1975. Acoustic profiling and sediment coring in Lake Ontario, Lake Erie and Georgian Bay. Geol. Surv. Can. Pap. 75-1, Part A: 373–376.

1985. Postglacial water-level history of the Lake Ontario Basin, p. 231–253. *In* P. F. Karrow and P. E. Calkin [ed.] Quaternary evolution of the Great Lakes. Geol. Assoc. Can. Spec. Pap. 30.

BOWLBY, J. R. 1975. Late glacial ice wedge casts in the Kingston Basin of Lake Ontario. M.Sc. thesis, Department of Geological Sciences, Queen's University, Kingston, Ont. 167 p.

BOWLBY, J. R., A. A. MOHAJER, AND R. K. MCMILLAN. 1988a. Observations of neotectonic conditions in western Lake Ontario. Abstracts with program, Int Assoc. Great Lakes Res. annual meeting, McMaster University, Hamilton, Ont. p. A5.

1988b. Neotectonic observations in the western Lake Ontario region and potential impacts on seismic hazard estimates. Abstracts with program, Geol. Assoc. Can. annual meeting, St. John's, Nfld. p. A13.

BOWLBY, J. R., R. L. THOMAS, O. L. WHITE, R. K. MCMILLAN, AND A. A. MOHAJER. 1988c. Observations of neotectonic features in western Lake Ontario region of the Laurentian Great Lakes of North America. Abstract, Methodology and Applications of Neotectonics Symposium, University of Orleans, Orleans, France.

BROOKFIELD, M. E., Q. H. J. GWYN, AND I. P. MARTINI. 1982. Quaternary sequences along the north shore of Lake Ontario, Oshawa – Port Hope. Can. J. Earth Sci. 19: 1836–1850.

CAMBRAY, F. W. 1987. Precambrian structure beneath the Michigan Basin. Abstracts with program, Int. Assoc. Great Lakes Res. annual meeting, Ann Arbor, MI.

1988. A tectonic model for the mid-continental rift system. Abstracts with program, 22nd annual meeting, North-Central Section, Geol. Soc. Am., Akron, OH. p. 338.

CANADIAN HYDROGRAPHIC SERVICE. 1970. Bathymetric chart No. 881 — Lake Ontario. 1:400,000 scale. Canada Department of Energy, Mines and Resources, Ottawa, Ont.

CHANDLER, V. W., AND G. B. MOREY. 1988. Seismicity and crustal structure in Minnesota, 1988. Abstracts with program, 22nd annual meeting, North-Central section of Geol. Soc. Am., Akron, OH. p. 339.

CHAPMAN, L. J., AND D. F. PUTNAM. 1984. The physiography of southern Ontario. Ont. Geol. Surv. Spec. Vol. 2: 270 p.

CLARK, R. H., AND N. P. PERSOAGE. 1970 Some implications of crustal movement for engineering planning. Can. J. Earth Sci. 7: 628–633.

COATES, D. R. 1981. Environmental geology. J. Wiley & Sons, New York, NY. 701 p.

COLEMAN, A. P. 1936. Geology of the north shore of Lake Ontario. Ont. Dep. Mines Annu. Rep. 45: 37–74.

ENVIRONMENT CANADA. 1975. Canada–Ontario Great Lakes shore damage survey. Minist. Nat. Resour. Tech. Rep. 97 p.

FAKUNDINY, R. H., J. T. MYERS, P. W. POMEROY, J. W. PFERD, AND T. A. NOWAK. 1978. Structural instability features in the vicinity of the Clarendon–Linden fault system, western New York and Lake Ontario. Solid Mechanics Study 13, University of Waterloo. p. 121–178.

GADD, N. E. 1980. Late-glacial regional ice-flow patterns in eastern Ontario. Can. J. Earth Sci. 17: 1439–1453.

GREEN, A., C. SPENCER, B. MILKEREIT, P. MOREL, A. DAVIDSON, J. BEHRENDT, W. CANNON, D. HUTCHINSON, AND M. LEE. 1987. Deep seismic surveys in the Great Lakes. Abstracts with program, Intern. Assoc. Great Lakes Res. annual meeting, Ann Arbor, MI.

GEOPHYSICS DIVISION, GEOLOGICAL SURVEY OF CANADA. 1987. Aeromagnetic total field maps 7333G (Rochester), 7334G (Toronto), 1:250,000 scale. Canada Department of Energy, Mines and Resources, Ottawa, Ont.

HARAS, W. S., AND K. K. TSUI [ED.] 1976. Canada/Ontario Great Lakes shore damage survey, Coastal Zone Atlas. Canada Department of the Environment, Ottawa, Ont.

HINZE, W. J., L. W. BRAILE, G. R. KELLER, AND E. G. LIDIAK. 1988. Tectonism in the Great Lakes region: an update. Abstracts with program, 22nd annual meeting, North-Central section of Geol. Soc. Am., Akron, OH. p. 348.

HOUGH, J. L. 1958. Geology of the Great Lakes. University Illinois Press, Urbana, IL. 313 p.

KARROW, P. F. 1967. Pleistocene geology of the Scarborough area. Ont. Dep. Mines Geol. Rep. 46: 108 p.

KASZYCKI, C. A. 1987. A model for glacial and proglacial sedimentation in the shield terrain of southern Ontario. Can. J. Earth Sci. 24: 2373–2391.

KELLY, R. I., AND I. P. MARTINI. 1986. Pleistocene glacio-lacustrine deltaic deposits of the Scarborough Formation, Ontario, Canada. Sediment. Geol. 47: 27–52.

KEMP, A. L. W., AND N. S. HARPER. 1976. Sedimentation rates and a sediment budget for Lake Ontario. J. Great Lakes Res. 2: 324–340.

KUMARAPELI, S. 1987. Seismic zones, ancient fault systems and post-glacial faulting in eastern Canada. Geol. Surv. Can. Open File Rep. 1617: 51 p.

KUMARAPELI, P. S., AND V. A. SAULL. 1966. The St. Lawrence valley system: a North American equivalent of the East African rift valley system. Can. J. Earth Sci. 3: 639–658.

LEWIS, C. F. M., AND P. G. SLY. 1971. Seismic profiling and geology of the Toronto waterfront area of Lake Ontario, p. 303–354. *In* Proceedings of the 14th Conference on Great Lakes Research. International Association for Great Lakes Research, Ann Arbor, MI.

LEYLAND, J. G., AND M. MIHYCHUK. 1984. Quaternary geology of the Trenton–Consecon area, southern Ontario. Ontario Geological Survey, map P.2586. Geological series preliminary map, scale 1:50,000. Geology 1980.

LIBERTY, B. A. 1960. Belleville and Wellington map-areas, Ontario. Geol. Surv. Can. Pap. 60–31: 9 p.

LOWMAN, P. D., JR., J. HARRIS, P. M. MASUOKA, V. H. SINGHROY, AND V. R. SLANEY. 1987. Shuttle imaging radar (SIR-B) investigations of the Canadian shield. Initial report to the IEEE. Trans. Geosci. Remote Sensing GE25(1): 55–66.

MARTINI, I. P., M. E. BROOKFIELD, AND Q. H. J. GWYN. 1984. Quaternary stratigraphy of the coastal bluffs of Lake Ontario east of Oshawa, p. 417–427. *In* W. C. Mahaney [ed.] Quaternary dating methods. Developments in palaeontology and stratigraphy. Elsevier, New York, NY.

MARTINI, I. P., AND J. K. P. KWONG. 1985. Nearshore sediments of Lake Ontario with special reference to the Presqu'ile–Wellington Bay area. Ont. Geol. Surv. Open File Rep. No. 5557: 99 p.

MCDONALD, B. C., AND W. W. SHILTS. 1975. Interpretation of faults in glaciofluvial sediments, p. 123–131. *In* A. J. Jopling and B. C. McDonald [ed.] Glaciofluvial and glaciolacustrine sedimentation. Soc. Econ. Paleontol. Miner. Spec. Publ. 23.

MCFALL, G. H., A. ALLAM, AND O. L. WHITE. 1989. Detailed investigations of neotectonic features in Prince Edward County, southwestern Ontario. Abstracts with Program., Geol. Assoc. Can. annual meeting, Montreal, Que.

MCFALL, G. H., AND O. L. WHITE. 1987. Structural geology of Prince Edward County, southern Ontario. *In* Summary of field work and other activities, 1987. Ont. Geol. Surv. Misc. Pap. 137: 596–597.

MCFALL, G. H., O. L. WHITE, AND G. A. GORRELL. 1988. Field investigation of neotectonic features in Prince Edward County, southern Ontario, Canada. Abstract, Methodology and Applications of Neotectonics Symposium, University of Orleans, Orleans, France.

MULLER, E. H., AND V. K. PREST. 1985. Glacial lakes in the Ontario Basin, p. 213–229. *In* P. F. Karrow and P. E. Calkin [ed.] Quaternary evolution of the Great Lakes. Geol. Assoc. Can. Spec. Pap. 30.

ONGLEY, E. D., J. G. RALSTON, AND R. L. THOMAS. 1977. Sediment and nutrient loadings to Lake Ontario: methodological arguments. Can. J. Earth Sci. 14: 1555–1565.

OTTO, J. E., AND R. W. DALRYMPLE. 1983. Terrain characteristics and physical processes in small lagoon complexes. Ont. Geol. Surv. Open File Rep. No. 5463: 89 p.

OWENS, E. H. 1979. The Canadian Great Lakes: coastal environments and clean up of oil spills. Environment Canada. Environ. Protect. Serv. Econ. Tech. Rev. Rep. 3-EC-79-2: 245 p.

PARRISH, J. B. 1988. Seismicity and lineament analysis of northwestern Ohio. Abstracts with program, 22nd annual meeting, North-Central section of Geol. Soc. Am., Akron, OH. p. 384.

PREST, V. K. 1970. Quaternary geology of Canada, p. 676–764. *In* R. J. W. Douglas [ed.] Geology and economic minerals of Canada. Geol. Surv. Can. Econ. Geol. Rep. No. 1: 676–764.

PRICE, C. A. 1954. Crustal movement in the Lake Ontario – St. Lawrence River basin. Canadian Hydrographic Service, Surveys and Mapping Branch, Department of Mines and Technical Surveys, Ottawa, Ont. 25 p.

QUITTMEYER, R. C., P. SOMERVILLE, K. A. MROTEK, K. HOULDAY, AND J. AGNEW. 1988. Focal mechanisms for two earthquakes near Lake Erie and Lake Ontario. Abstracts with program, 22nd annual meeting North-Central section of Geol. Soc. Am., Akron, OH. p. 385.

RUKAVINA, N. A. 1976. Nearshore sediments of Lakes Ontario and Erie. Geosci. Can. 3: 185–190.

SANFORD, B. V., F. J. THOMPSON, AND G. H. MCFALL. 1985. Plate tectonics — A possible controlling mechanism in the development of hydrocarbon traps in southwestern Ontario. Bull. Can. Petrol. Geol. 33: 52–71.

SINGER, S. 1974. A hydrogeological study along the north shore of Lake Ontario in the Bowmanville–Newcastle area. Ont. Minis. Environ. Water Resour. Rep. 5d: 72 p.

SINGHROY, V. H. 1988. Case studies on the application of remote sensing data to geotechnical investigations in Ontario, Canada, p. 9–45. *In* A. I. Johnson and C. B. Peterson [ed.] Geotechnical applications of remote sensing and remote data transmission. ASTM STP 967. American Society for Testing and Materials, Philadelphia, PA.

SLY, P. G. 1977. Sedimentary environments in the Great Lakes, p. 76–82. *In* H. L. Golterman [ed.] Proc. SIL-UNESCO Symp. Interactions between sediments and fresh water. Junk, Amsterdam, The Netherlands.

1980. Sedimentary processes in Lakes, p. 63–69. *In* A. Lerman [ed.] Lakes, chemistry, geology and physics. Springer-Verlag, New York, NY.

1983a. Sedimentary and geochemistry of recent sediments off the mouth of the Niagara River, Lake Ontario. J. Great Lakes Res. 9: 134–195.

1983b. Recent sediments stratigraphy and geotechnical characteristics of foreset and bottomset beds of the Niagara Bar. J. Great Lakes Res. 9: 224–233.

1984. Sedimentology and geochemistry of modern sediments in the Kingston basin of Lake Ontario. J. Great Lakes Res. 10: 358–374.

1986. Review of postglacial environmental changes and cultural impacts in the Bay of Quinte. *In* C. K. Minns, D. A. Howley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorous control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

SLY, P. G., AND C. F. M. LEWIS. 1972. The Great Lakes of Canada — Quaternary geology and limnology. XXIV Int. Geol. Congr., Excursion A43, Montreal, Que. 148 p.

SLY, P. G., AND J. W. PRIOR. 1984. Late-glacial and post-glacial geology in the Lake Ontario basin. Can. J. Earth Sci. 21: 802–821.

SLY, P. G., AND R. L. THOMAS. 1974. Review of geologic research as it relates to an understanding of Great Lakes limnology. J. Fish. Res. Board Can. 31: 795–825.

SPENCER, J. W. 1890. Origin of the basins of the Great Lakes of North America. Am. Geol. 7: 86–97.

SUTTON, R. G., T. L. LEWIS, AND D. L. WOODROW. 1970. Nearshore sediments in southern Lake Ontario, their dispersal patterns and economic potential, p. 308–318. *In* Thirteenth Conf. Great Lakes Res., Buffalo, NY.

SUTTON, R. G., AND D. L. WOODROW. 1972. Post-Iroquois Lake stages and shoreline sedimentation in eastern Lake Ontario Basin. J. Geol. 80: 346–356.

THOMAS, R. L., A. L. W. KEMP, AND C. F. M. LEWIS. 1972a. Report on the surficial sediment distribution of the Great Lakes. Part I — Lake Ontario. Geol. Surv. Can. Pap. 72-17: 52 p.

1972b. Distribution, composition and characteristics of the surficial sediments of Lake Ontario. J. Sediment. Petrol. 42: 66–84.

THOMAS, R. L., R. K. MCMILLAN, D. L. KEYES, AND A. A. MOHAJER. 1989. Surface sedimentary signatures of neotectonism as determined by side-scan sonar in western Lake Ontario. Abstracts with program, Geol. Assoc. Can., annual meeting, Montreal, Que.

THOMAS, R. L., AND P. G. SLY. 1988. Lake Ontario sediments. Abstracts with program, Int. Assoc. Great Lakes Res., 31st annual meeting, McMaster University, Hamilton, Ont. p. A54.

WALL, G. J., W. T. DICKINSON, AND L. J. P. VAN VLIET. 1982. Agriculture and water quality in the Canadian Great Lakes Basin: II. Fluvial sediments. J. Environ. Qual. 11: 482–486.

Physical Behaviour of Lake Ontario with Reference to Contaminant Pathways and Climate Change

F. M. Boyce, W. M. Schertzer, P. F. Hamblin, and C. R. Murthy

Environment Canada, National Water Research Institute, Canada Centre for Inland Waters, 867 Lakeshore Road, Burlington, Ont. L7R 4A6, Canada

Boyce, F. M., W. M. Schertzer, P. F. Hamblin, and C. R. Murthy. 1991. Physical behaviour of Lake Ontario with reference to contaminant pathways and climate change. Can. J. Fish. Aquat. Sci. 48: 1517–1528.

Current understanding of the physical behaviour of Lake Ontario is assessed. In particular, the role of water movements in the distribution and fate of contaminants is described, and our ability to anticipate the results of global climate warming on the Great Lakes is surveyed. In the past two decades, the general features of large-lake circulation and mixing have been successfully delineated, although detailed climatological studies will be required for particular sites of interest or concern. More sophisticated models of thermal structure will be needed to assess the potential consequences of climate warming, particularly in the matter of convective overturning. The process of "sediment focusing," so strongly linked to the fate of many organic contaminants, is only recently amenable to study with instruments that respect the time and space scales of resuspension and settling. The rates of transfer of gases and contaminants across the air–water interface are known to depend on wind and wave conditions; this dependence is being explored. Experience over the past 20 yr has consistently shown that large-lake studies of chemical and biological processes are difficult if not impossible to interpret in the absence of an adequate base of concurrent physical measurements.

On présente une évaluation des connaissances actuelles sur le comportement physique du lac Ontario. On décrit en particulier le rôle de la circulation des eaux dans la distribution et le devenir des contaminants, et on examine la capacité de prévoir les répercussions du réchauffement de l'atmosphère sur les Grands Lacs. Au cours des deux dernières décennies, les principales caractéristiques de la circulation et du mélange à grande échelle ont été décrites avec succès quoique des études climatologiques détaillées seront nécessaires dans le cas d'endroits étant sujets d'un intérêt ou d'une inquiétude particuliers. Des modèles plus sophistiqués de la structure thermique seront nécessaires pour évaluer les conséquences possibles du réchauffement de l'atmosphère, surtout pour ce qui est du renversement de la convection. Le processus de « concentration des sédiments », fortement lié au devenir d'un grand nombre de contaminants organiques, n'est que depuis peu facile à étudier avec des instruments qui tiennent compte des échelles temporelles et spatiales de la sédimentation et de la remise en suspension. On sait que les taux de transfert des gaz et des contaminants à l'interface air – eau dépendent des vents et des vagues et cette relation fait l'objet d'une étude. L'expérience recueillie au cours des 20 dernières années a régulièrement démontré que les résultats d'études des processus chimiques et biologiques sont difficiles, sinon impossibles, à interpréter en l'absence d'une base adéquate de caractères physiques simultanés.

Received March 3, 1989
Accepted March 21, 1991
(JA074)

Reçu le 3 mars 1989
Accepté le 21 mars 1991

Recent advances in the understanding of both large- and small-scale physical processes in the Great Lakes have been reviewed (Boyce et al. 1989; Csanady 1984); monographs by Simons (1980a) and Csanady (1982) summarize the relevant theory. A critical review of the lake system modelling (biology plus chemistry plus physics) carried out under the leadership of T. J. Simons has been published (National Water Research Institute (NWRI) 1988). These documents provide a concise and current summary of both the application and theory of large-lake physics.

This paper provides an overview of the central themes of physical limnology as they relate to the concerns of biology and chemistry reported elsewhere in this volume. We present first a brief statement of the consequences of the simultaneous presence of phenomena operating over a continuum of time and space scales. Next we describe the thermal structure of Lake Ontario because of its importance in defining or controlling ecological niches. Then we present an overview of wind-driven water movements, the agents of internal redistribution of dissolved and suspended materials. In the remaining two sections of the paper, we discuss the physical components of two major environmental concerns, the pathways and fate of toxic contaminants and the response of the lake to the anticipated global warming. The paper points out that large-lake measurements unsupported by appropriate physical insights and data may be impossible to interpret and thereby argues for a multidisciplinary approach.

Time and Space Scales: Numerical Simulations

Lake systems operate in a continuum of time and space scales. Time scales of concern to the study of Lake Ontario range from the geological (10 000 to 100 000-yr ice-age cycles) to a scale of seconds associated with small-scale turbulence. Prominent in this large range are the seasonal or annual cycles, the average time between major meteorological events (several days), and the daily cycle. It is not always possible to disassociate the effects of one cycle or time scale from those of another. In this present review, we are particularly concerned with "long-term" trends in lake behaviour extending over many

years where the annual increment of change associated with the trend is very much smaller than the changes imposed by the annual cycle or indeed by the substantial year-to-year variability in the annual cycles themselves. Reliable detection of trends or other long-term variations in "noisy" data requires a minimum length of record that depends both on the sampling methods and on the variability of the data. Unless the sampling methods and subsequent interpretations allow properly for all possible sources of variability, trends may be wrongly inferred (Charlton 1980).

Spatial scales of water movements range from centimetre-scale turbulence to the dimensions of the basin itself, and even larger scales are associated with weather systems. At any point in the lake, the controlling spatial dimensions are those of the basin itself and the distance of the point from each of several important boundaries (shore, bottom, surface, thermocline). For most problems having to do with the whole lake, horizontal variations taking place over kilometres and vertical variations over 5–10% of the water depth would be of most interest, but smaller scale motions cannot be ignored, since they may contribute significantly to mixing processes. Moreover, the small-scale motions appear random or chaotic in nature, and although their mean properties are usually assumed to be related to the large-scale flow and to rates of energy loss to friction, the nature of such parameterizations is still a subject for research and debate.

Because the laws of fluid motion are generally known and expressible as a set of partial differential equations that can be solved for the flow field in both time and space, much effort has been expanded in developing computer-based models that simulate fluid motion in terms of boundary conditions, externally applied forces, and the initial state of motion. Despite the enormous computing power of today's machines, practical realities limit the models to relatively coarse resolution in both time and space. The problem of parameterizing the influence of smaller scale motions on the scales of motion resolvable by the model limits the accuracy of such simulations. Numerical simulations have nevertheless been extremely useful in developing and confirming physical insight. It is natural to turn to such models as a tool for predicting the future behaviour, but here an even more fundamental difficulty limits the length of time a prediction or forecast can be projected into the future (Lorenz 1969). The initial conditions specified as input to the model are an approximation to the "true" initial conditions by virtue of measurement errors and the filtering imposed by the model structure. The difference between "true" and imposed initial conditions constitutes an unknown "error" signal, and work pioneered by Lorenz (1969) showed that this error signal is invariably amplified by the model and eventually masks the predicted changes. This effect is well known to meteorologists but its consequences do not seem to have been understood in other related disciplines. Our concern, however, is less with the hour-by-hour prediction of detailed flow fields and more with the development of what might be termed a climatology of lake behaviour for which the limitations described by Lorenz (1969) may be less severe but present, nevertheless. A recent article by Tennekes (1988) described this quandary and recommended a more realistic philosophy for the making or using of forecasts of the behaviour of multi-scaled systems.

Annual Thermal Cycle in Lake Ontairo

Lake Ontario stratifies regularly and reliably each year and exhibits two periods of convective overturn, one in spring and one in autumn during which it appears that the lake is mixed from top to bottom. The details of the thermal cycle, such as the dates of onset and disappearance of stratification and thicknesses of the upper mixed layer and the thermocline region through the stratified season, are subject to significant spatial and temporal variation. Since nutrient availability and biological productivity are closely tied to both absolute temperature and thermal structure, physical effects must be accounted for before biochemical effects can be deciphered in the observational record (Simons and Schertzer 1987). The prospect of significant global increase in the earth's surface temperature in the coming decades has motivated substantial and increasing efforts to develop plausible scenarios of the lake's responses, particularly those affecting its thermal structure. This will be more fully discussed later.

Lakewide Effects: Whole-Basin Approach

One of the principal scientific goals of the International Field Year on the Great Lakes (IFYGL) (1972–73) was to evaluate all possible terms in the annual heat and water budgets of Lake Ontario in order to define the lakewide evaporative heat flux with greater precision. During this experiment, Lake Ontario served as a huge calorimeter. The results of this study are summarized in the IFYGL synthesis volume (Aubert and Richards 1981). The IFYGL data set, the most complete at the time, greatly stimulated the development of lake simulation modelling (Simons 1974, 1975, 1976). Despite the appeal of fully three-dimensional models with many biological and chemical compartments, it has been found that the greater accuracy promised by more realistic simulations was not fully realized because the transfers across the growing number of interfaces were not generally known and had to be parameterized often in arbitrary ways (Simons and Lam 1980). Relatively simple "box" models of whole lake basins are more suitable for the level of knowledge we now possess, and the physical armature for these models is a one-dimensional thermodynamic model. In addition, these more simple models are computationally more economical than the more complex three-dimensional approaches, a distinct advantage for climatological studies.

Modern thermodynamic modelling of lakes may be classified into two approaches, empirically based models and integral models. A good example of the empirical approach is provided by Baba's (1974) study of the thermal cycle of Lake Ontario in which he derived eddy mixing coefficients from field measurements of thermal structure and introduced tracers that are subsequently used to "predict" evolving thermal structure. A more recent example of the empirical approach is found in the work of Henderson-Sellers (1985). In small lakes and in shallow lakes, the arbitrary specification of eddy diffusivities was successful, since in these water bodies the thermal structure is dominated by vertical convection and less by vertical diffusion. In contrast, the thermal properties of larger, deeper lakes are more strongly influenced by diffusion processes (Harleman 1986). In these situations the performance of ad hoc thermocline models has not been satisfactory and this has led to the development of a more exacting parameterization of thermal diffusion based on both turbulence theory and field and laboratory experiments.

Eddy diffusivities are often specified as the product of a mixing length scale and a turbulent velocity scale characteristic of the flow. A review of various formulations for these scales is given in Blumberg (1986). One approach, the so-called k–ϵ

turbulence model, has been applied to the seasonal development of thermal stratification by Svensson (1978). The simulation of thermal structure was acceptable for the epilimnion, but in obvious error within the hypolimnion, since, in the model, that portion of the water column remained at winter temperatures throughout the year. Clearly, the weak, but important mixing processes within the hypolimnion were not properly simulated.

The integral approach is also semiempirical and it is based on the temporal evolution of the vertical integral of the turbulent kinetic energy budget. Details of the energy transfers in the mixed layer have been adapted from the oceanographic literature (Pollard et al. 1973). A major improvement of the integral models, as applied to lakes, was the parameterizing of the shear-induced mixing at the thermocline powered by internal waves (Spigel and Imberger 1980). Ivey and Patterson (1984), in simulating the thermal structure of Lake Erie's Central Basin, further improved the model by accounting for the turbulent energy generated by bottom friction in a bottom mixed layer. In this special case, the bottom-generated turbulence is derived from observations of bottom currents and an estimated bottom drag coefficient. In other situations, a limited turbulent energy budget is formulated for the subsurface waters in order to simulate the observed vertical mixing. Hamblin et al. (1987) has compared the approach of Fischer et al. (1979), where the dissipation rate of turbulent kinetic energy is assumed to be independent of depth, with that of Harleman (1986), who considered the dissipation to depend on the local stability of the water column. Hamblin et al. (1987) found that the second approach leads to more accurate simulations, especially during periods of weak stratification in the spring and fall seasons. Improved understanding of the vertical diffusion of heat and dissolved or suspended materials is a valid goal for further research.

The inclusion of the effects of snow and ice cover represents another significant advance in the thermal modelling of lakes. Patterson and Hamblin (1988) have developed and tested formulations for snow and ice cover on data from large, deep lakes in British Columbia and in the Yukon Territory. These formulations should be verified in the Great Lakes.

Another important effect in deep, high-latitude lakes is that of the compressibility of water. Remarkable consequences on thermal structure evolve from the fact that warm water is more compressible than cool water; these are explored in the modelling study of McCrimmon and Hamblin (1988). A sample temperature profile from their study (Fig. 1) shows a situation that might occur after the mixing of two horizontally adjacent water masses initially at two temperatures below the temperature of maximum density. Because of compressibility effects, there exists a depth at which both initial water masses have the same density, termed "compensation depth" in their study. Mixing occurs both above and below this depth and the resulting temperature profile possesses an extremum near the compensation depth.

Thermal modelling concepts dealing with small but important changes in water density imposed by pressure or dissolved or suspended materials are usefully extended to water quality concerns such as total and dissolved solids (Wei and Hamblin 1986; Hollan et al. 1990). All of these processes are at various times and places important in Lake Ontario. Incorporation of them into, for example, a simulation of the lake's response to anticipated climatic change remains high on the agenda of work to be done.

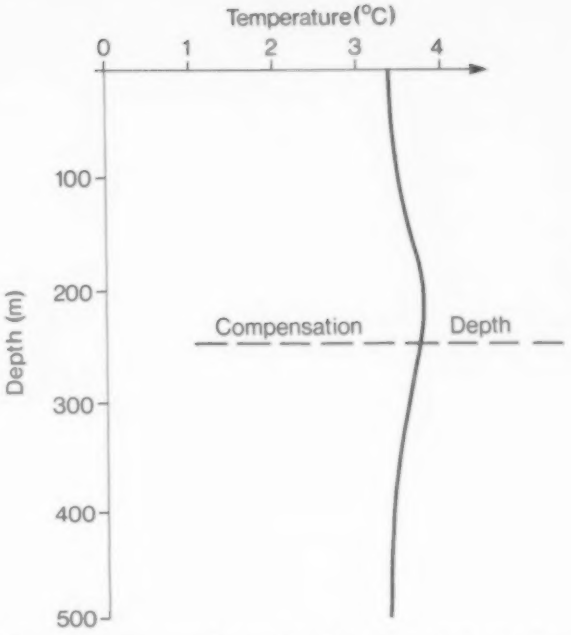


FIG. 1. Temperature profile resulting from the gravitational collapse of two initially homogeneous water columns at two temperatures at or below the temperature of maximum density (McCrimmon and Hamblin 1988).

Nearshore Effects

Whereas for practical purposes, thermal energy both enters and leaves the lake at the air-water interface, mechanical mixing processes allow a much larger thickness of the water column to participate in the daily cycle of heating and cooling. In the nearshore shallow regions of the lake, the "zone of participation" often extends to the bottom. This is also true for the transfer of the momentum of the wind to the water, as will be discussed later. In the early spring, prior to whole-lake stratification, when the lake is at temperatures close to 4°C (temperature of maximum density of freshwater), density-driven horizontal water movements are weak because of the small coefficients of thermal expansion. The effective heat capacity of the water column is proportional to local water depth. The nearshore zone warms to temperatures above 4°C more quickly than the offshore water, and the convergence and sinking of water near the temperature of maximum density ensures that the horizontal boundary between warm nearshore water and cool offshore water remains sharp. This phenomenon, called the "thermal bar," lasts for several weeks in Lake Ontario (Zilitinkevich and Terzhevik 1987; Rodgers 1987; Schertzer and Sawchuk 1990; Ivey and Hamblin 1989), and during this time the large flux of nutrients from spring runoff remains "trapped" in the warm water on the nearshore side of the thermal bar. High nutrient levels and warm temperatures result in increased biological productivity. As the nearshore water continues to warm differentially with respect to the open lake, the onshore/offshore density differences become dynamically significant, and the warm water tends to move offshore and spread over the cool open-lake water. The time scale of this process being long, the offshore-moving warm water is deflected by

Coriolis force to the right of its direction of motion forming a counterclockwise circulating band of warm water at the edge of the lake. This thermally driven circulation may persist well into summer (Bennett 1971). The pathways and fates of contaminants introduced into the nearshore zone during the thermal bar period in the presence of elevated concentrations of biota, nutrients, and suspended material must be different from those occurring at other times, a topic worthy of study in view of its connections to management issues (Taylor et al. 1987).

In small lakes that exhibit seasonal stratification, water lying beneath the upper mixed layer (metalimnion and hypolimnion) is "sealed off" from exchanges with the atmosphere by virtue of the stability of the water column and the limited amount of mechanical energy that can be extracted from the wind. It can be demonstrated (Spigel and Imberger 1980; Imberger and Hamblin 1982; Gorham and Boyce 1989) that for a given wind impulse, the mechanical energy available to displace the thermocline is an increasing function of the horizontal dimensions of the basin up to the point where Coriolis force dominates the transient response of water motions in response to changing winds. The Great Lakes, Lake Ontario in particular, fall into the latter category, behaving more like the coastal oceans. Thus, a combination of wind stress and Coriolis force may be sufficient to move warm nearshore water away from the shore and to allow cooler subsurface water to upwell. The northwest shore of Lake Ontario is prone to episodic wind-driven upwellings of cool metalimnion water, while the southeast shore experiences the concomitant downwelling (Simons and Schertzer 1987). Again, these motions have consequences for biological productivity.

Wind-driven Water Movements

Wind contributes mechanical energy to the water in three ways, through the creation of disorganized turbulence, through the creation of a surface gravity wave field, and through the creation of organized, horizontal currents. There are interactions among all three types of motion, particularly between turbulence and mean motion, since it is the turbulence which transfers the stress exerted by the wind on the water surface to the subsurface layers. In a homogeneous water column, surface-generated turbulence can penetrate to the bottom, although energy is continually dissipated to heat throughout the turbulent field. When the lake is stratified, vertical turbulent motion must overcome the gravitational stability of the stratified regions (lift cool water up, push warm water down) and may consequently be attenuated where the vertical density gradients are large. Away from the shore, organized, large-scale currents are thus initially confined to the upper mixed layer or epilimnion. However, the strong shearing motion that develops between the actively driven upper layer and the quiescent lower layer is also a potential source of mixing energy at the level of maximum shear through the mechanism of dynamic instability (Spigel and Imberger 1980). Thus, large-scale motion or mean currents may contribute to turbulent mixing under the appropriate conditions (see earlier paragraphs on thermodynamic modelling). The surface wave field may also contribute to the turbulence and mixing in the upper layers through random wave-breaking and/or bottom shear, creating a connection between the characteristics of the wave field and the local wind stress. This connection together with its implications for the transfer of heat and mass (gases, contaminants) across the water surface is an important and active field of research worldwide, with many pioneering results coming from work on Lake Ontario (Donelan 1989). Models of vertical mixing, such as the thermocline models mentioned earlier, must take into account in explicit or implicit fashion the interactions among all the types of motion listed above.

Large-scale horizontal turbulence and currents are of particular interest because of their potential for distributing dissolved and suspended materials. It must be emphasized that horizontal motions occupy a continuous spectrum of spatial scales, the largest of which represents the cross-lake dimensions of the basin. The initial response of a closed basin to a suddenly imposed wind has some parallels with the thermal bar situation discussed earlier in that the total inertia of the water column responding to the wind stress is proportional to either the water depth or the depth of the actively stirred layer. Thus, currents at the shoreline parallel to the direction of the suddenly imposed wind accelerate downwind near the shore, with a compensating upwind transport in the deep water of midlake (Bennett 1974). In both stratified and unstratified conditions, this initial circulation results in an extended transient response in the form of wavelike disturbances that propagate counterclockwise around the basin. The reader is referred to the review documents and monographs mentioned earlier for an explanation of the wave mechanisms. The signature of such basin-scale waves at a point near the shore is first a component of current alongshore in the direction of the alongshore component of the wind, followed by a reversal of current some days later. The zone of current reversal propagates counterclockwise around the shore of the basin (Csanady 1982) at speeds of the order of 20 km/d. This response is confined to within 10 km of the shore, a region sometimes called the coastal boundary layer. During the stratified season the currents are associated with vertical displacements of the thermocline (upwellings and downwellings), but vertical motions of water occur near the shore even more vigorously during the homogeneous period. Current reversals are also associated with large onshore/offshore exchanges of water. These coastal currents move parallel to the shore for several days (excursions of tens of kilometres) and then reverse and flow the other way for comparable, if unequal, periods. During the intervals of unidirection, shore-parallel flow, onshore/offshore mixing may be weak, and effluent from an outfall, for example, may be carried tens of kilometres along the shore with relatively little dilution. The water exchanges associated with the flow reversals tend to "wipe the coast clean."

While flow reversals have beneficial aspects from the point of view of the dispersal of pollutants in the coastal region, there are other events such as periods of very low currents (less than 5 cm/s) or stagnation producing detrimental effects because of weak dispersal. The siting of effluent discharges along the coastline is undoubtedly dictated, among other things, by the climatology of coastal currents (Csanady 1970, 1971; Murthy 1972). Considerable progress has been made over the years to develop effluent transport and diffusion models for the coastal zone based on knowledge of the complex physical processes acquired through theoretical and experimental investigations. For further information, the reader is referred to the monograph by Lam et al. (1984).

The open-lake transient response is very much like the response to be expected in the open ocean; when the basin is stratified, the surface currents tend to move in circles with a frequency of one cycle roughly every 16 h. The circular motion is a direct consequence of the earth's rotation (Simons 1980a).

Although the transient response of large-scale lake currents to wind can be simulated reasonably well by simple linearized numerical hydrodynamic models over short time scales (a few days), the accuracy of longer term predictions remains poor, mainly because, as it turns out, the linearized model neglects subtle but important feedback processes. In a particularly well-planned field experiment, Simons et al. (1985) were able to demonstrate the existence of a substantial residual circulation comprising a fast belt of current moving east near the south shore of the basin balanced by a more diffuse and slower return flow to the west in midlake. The flux of this current in one direction is roughly equal to 10 times the flow of the Niagara River entering Lake Ontario. Simons was able to simulate the structure of this residual flow when he introduced nonlinear acceleration terms into his dynamic model. The residual gyre is in effect the rectification of large-amplitude wavelike flows. One direct implication is that the Niagara River, which often flows into this eastward moving residual boundary flow, is rapidly recirculated within the lake, with a mixing time scale that is only a few weeks. The combined effect of the continuum of scales of motion is graphically demonstrated by satellite-tracked drifter experiments (Simons et al. 1985). The accurate fixes on drifter positions obtained several times a day reveal not only the residual current described above, but also more irregular motion associated by the response of the currents to the individual pulses of wind. The distribution of mercury and Mirex, emanating from known sources on the south shore of Lake Ontario and now located in the sediments, is consistent with alongshore displacement by the residual current plus lateral mixing accomplished by the transient and small-scale motions.

Interaction among Water Movements and the Pathways and Fates of Dissolved and Suspended Contaminants

The severity of the contaminant problem is ultimately judged by the distribution of the contaminants in living creatures and the damage they do there. Although it is fundamentally a biological problem, the pathway of a contaminant from its source to the biota, together with the mechanisms for removal or alteration, may involve physical as well as chemical and biological processes. Experience has shown that attempts to measure contaminant budgets and fluxes in the field without accounting for physical processes of transport lead to ambiguous results (Royer et al. 1987), particularly in large, horizontally nonhomogeneous lakes such as Lake Ontario. Not only do we require a basic understanding of the various physical processes acting to distribute contaminants, but we also need to maintain the ability to measure these processes in support of chemical and biological field experiments.

Ignoring for the moment the processes that would remove contaminants from the water column (sedimentation, chemical or biological alteration), the distribution of contaminants introduced at the shores from rivers, outfalls, or distributed runoff depends on the water motions discussed above. Existing information is sufficient to describe the gross properties of large-scale redistribution using circulation models (Simons and Lam 1978). Detailed work along these lines has been conducted in support of the Niagara River study (Murthy et al. 1986).

The Niagara River, with a long-term (1860–1989) monthly mean discharge ranging from 3280 to 7590 m/s, furnishes approximately 83% of the total annual input of water to Lake Ontario (P. Yee, pers. comm.; Coordinating Committee on Great Lakes Basic Hydraulic and Hydrologic data (CCHD) 1976). This same river also supplies approximately 4.7 million tons of sediment annually, 52% of the total sediment load to the lake (Mudroch 1983). Industries and municipalities along the Niagara River discharge liquid wastes into it while at the same time, both the river and the lake immediately downstream are sources of drinking water and sites for recreation and tourism. Degradation of the Niagara River and Lake Ontario has been a focus of public anxiety for several decades.

In recent years, in both the United States and Canada, there has been much concern about the transport, distribution, and pathways of toxic contaminants entering the lake from the Niagara River. An integrated, multidisciplinary study was undertaken to examine the toxic contaminants problem in the Niagara River/Lake Ontario system. In the years 1982–86, simultaneous experiments were undertaken to delineate (i) the transport and mixing of the river plume in the lake and (ii) the distribution, in both water and sediments, of selected contaminants associated uniquely with the Niagara River inflow. This information aided the development of hydrodynamic models of the river plume behaviour in the lake, and these models in turn formed the basis of a transport model that simulated the distribution and pathways of selected contaminants (Murthy et al. 1986; Stepien et al. 1987). The compartmental distribution and transport of toxic materials in the vicinity of the Niagara River plume was simulated using a simple partitioning hypothesis. Figure 2 demonstrates a successful model simulation for August 10, 1983, illustrating the current and velocity fields (Fig. 2a) and a corresponding typical distribution pattern for concentrations of 1,2,4-TCB (Fig. 2b) under assumed conditions of sediment settling velocity, river inflow, and diurnal variations of flow and concentration. The results have clearly shown that such models may be used for the purposes of nearshore and short-time prediction of the fate and transport of toxic chemicals in the coastal zone. The approach offers a framework within which more detailed processes or boundary conditions can be incorporated to analyse coastal environmental problems in the Great Lakes.

Contaminants such as PCB's enter the lake through several pathways. For Lake Ontario, total inputs of PCB's are estimated to be 2540 kg/yr, of which 178 kg, or 7% of the total, is attributed to atmospheric loading. In comparison, some 90% of the total load of PCB's (606 kg/yr, total) to Lake Superior comes from the atmosphere (Strachan and Eisenreich 1987). Since the time scales of vertical mixing within the wind-stirred layer are relatively short compared with those of horizontal redistribution (hours compared with days or weeks), relatively simple layered models of horizontal transport may still be applicable. The models of thermal structure discussed earlier can be adapted to simulate the mixing of contaminants from the surface down through the water column. Nevertheless, the overall problem of modelling PCB redistribution is complicated further because substantial fractions may be lost from the lake surface by volatilization.

The tendency for many organic contaminants to bind preferentially to suspended particles (Allan 1986) means that in addition to transport and dilution by water movements, the distribution and fate of contaminants are influenced by the physical processes of erosion, resuspension, flocculation, and settling.

Zooplankton and phytoplankton produced in the lake itself are major sources of particulate material, dusts and pollens are carried by the wind, and beach erosion and runoff from the land

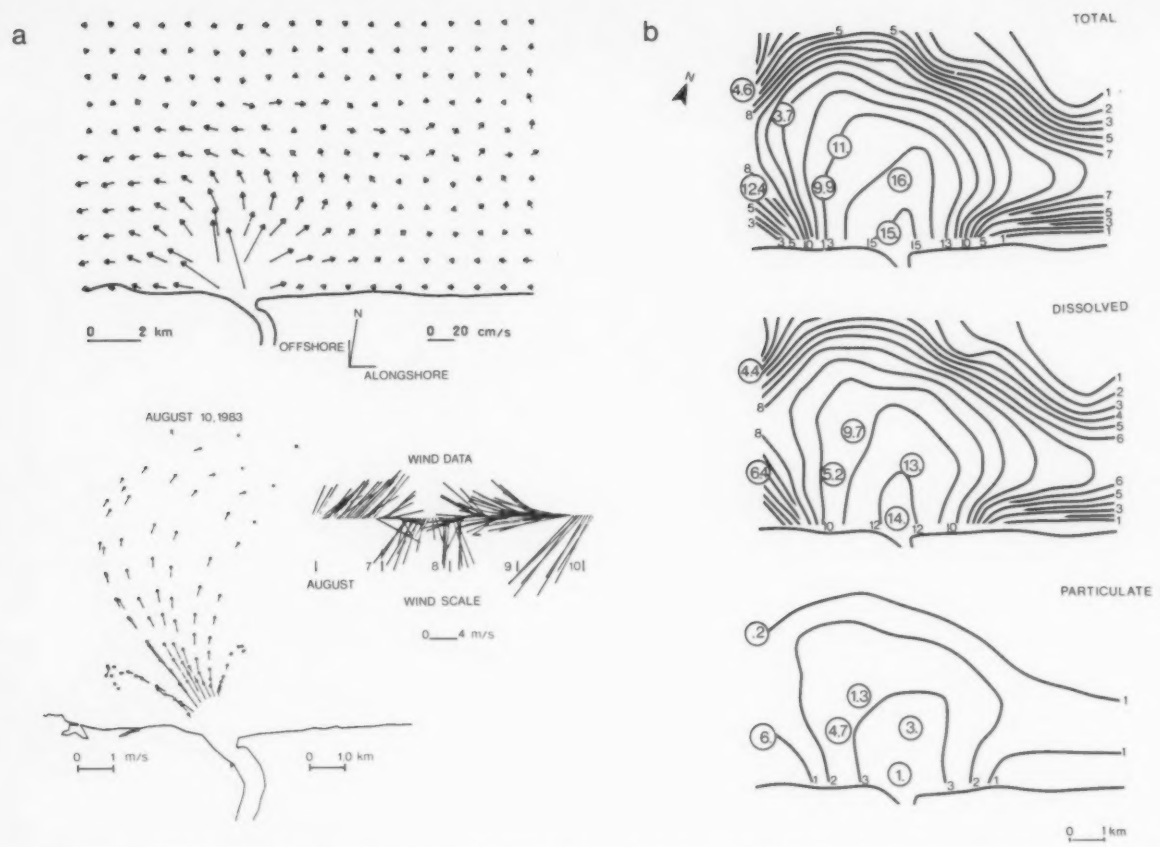


FIG. 2.(a) Vertically integrated current field for 14:00 GMT, August 10, 1983, as derived from the hydrodynamic model (top panel) and horizontal current velocities deduced from drogue trajectories for the same time (lower panel). (b) Computed (contours) and observed (circles) concentrations of 1,2,4-TCB (ng/L) (total (upper panel), dissolved (middle panel), and particulate (lower panel)) for August 10, 1983. Figures originally published by Stepien et al. (1987) and reproduced with the authors' permission.

contribute still more. For example, Rukavina and Zeman (1987) estimated that silt-clay glacial sediments exposed to littoral currents and to wave orbital motions may contribute as much as 15% of the total sediments eroded from shore bluffs along the north-central shore of Lake Erie. Considering that each sediment type can differ in its affinity for a particular contaminant, an important area for research is the physics and chemistry of the partitioning of contaminants between the water and the suspended material. Successful modelling of the transport and fate of contaminants in the presence of suspended materials depends on this knowledge.

A key parameter in describing the behaviour of suspended material is the settling velocity of the particles. This rate determines the average residence time of the particle in the water column under calm conditions, and this residence time can be usefully compared with time scales of vertical and horizontal mixing, average time between major storms, etc., in order to assess the relative importance of each process in determining particle distributions. A single "average" settling velocity is a very crude parameterization of what must in nature be a wide spectrum of settling speeds, and moreover, it is known that the process of flocculation, itself dependent on the energy levels of small-scale turbulence, greatly affects actual settling speeds (Tsai et al. 1987).

The preparation of samples for the laboratory determinations of settling speeds is known to affect the results. Sample treatment includes mechanical and chemical dispersion (Duncan and LaHaie 1979) which reduces sediment to individual particles, and in the process breaks up the original aggregates from suspension as well as those formed by contact of the particles as they accumulated on the bottom or in settling traps. The resultant settling velocity distribution is distorted but reproducible; this is the rational for this form of analysis. True settling velocity data will require in situ tracking of settling particles, and work is underway at NWRI to develop an optical technique (B. Krishnappan, NWRI, Burlington, Ont., pers. comm.). In the absence of more refined techniques that yield realistic weighted spectra of in situ settling speeds, modelling of the settling process must remain at a primitive, order-of-magnitude level.

The actual progress of a particle from point of introduction to either final burial or to the outlet of the basin may be discontinuous. While very fine particles with low settling speeds may never settle appreciably from the water column, and are carried instead to the outflow or modified by processes occurring within the water column, coarser particles may settle to

the bottom near to their source, only to be resuspended and transported during the next storm, tending eventually to accumulate in regions of the basin where the energy of the water movements is insufficient to resuspend them again (sediment focusing). Each time the particle is resuspended into the water column, it may exchange contaminants with the water, depending on the relative concentrations and the partitioning coefficients. This effect can be expected to increase the effective residence time of the contaminant in the system. Thus the physical process of sediment resuspension is likely to influence the pathways and fate of sediment-bound contaminants in lakes.

The source of energy for the resuspension of sediment is the movement of water near the bottom. In a recent review, Bedford and Abdelrhman (1987) discussed the nature of the bottom boundary layer in relation to sediment resuspension. The nature of the boundary layer depends on the time-variability of the forcing currents as well as on the nature (roughness) of the bottom material. In Lake Ontario, the oscillating motion and pressures induced by surface waves with periods of several seconds will govern sediment resuspension in shallow waters, in contrast with the steadier Ekman-like boundary layer obtained in deep water (Saylor and Miller 1988). The structure of the boundary layer in steady flow conditions is reasonably well understood, but the experimental difficulties associated with the small temporal and spatial scales of the wave-dominated boundary layer (centimetres and seconds) have delayed the verification of existing theories. Relating the boundary layer structure to sediment resuspension via an appropriate average of the bottom stress, for example, remains at the level of very crude parameterization (Simons and Schertzer 1986) for lack of simultaneous and detailed measurements of suspended sediment concentrations and water movements near the bottom. This problem has received much attention in the oceanographic community, and only now are the measurement techniques evolving to the point where theories can be tested and improved. The situation is further complicated by the variability of the mechanical properties of the sediments themselves (Lick and Kang 1987; Tsai and Lick 1986; White et al. 1987), including the effects of benthic organisms. Within the Great Lakes, work by Chambers and Eadie (1981), Rosa (1985), Lesht and Hawley (1987), Hamblin et al. (1989), and Bedford et al. (1983) has addressed various aspects of this problem.

It is known that much of the contaminant flux to the Great Lakes is from the atmosphere, and it is suspected that the more volatile forms may return to the air from the lake. Mass transfer of contaminants across the water surface is again a problem occupying both oceanographers and limnologists and requires on the physical side an understanding of how surface waves may affect such transfers.

Anticipating Lake Ontario's Response to Global Warming

A growing consensus among climate modellers is that global air temperatures will rise with increasing concentrations of atmospheric greenhouse gases such as carbon dioxide, methane, nitrous oxide, and freons (Canadian Climate Centre (CCC) 1986; Hansen et al. 1981). Simulations of potential climate changes resulting from a doubling (or quadrupling) of atmospheric carbon dioxide concentrations have been performed using general circulation models (GCM's). For the Great Lakes region, such models generally predict a warming of 3.2–4.8°C (Maarouf 1985) scenarios of a doubling under of carbon dioxide (Hansen et al. 1984), and such responses are expected to occur within 40–50 yr. A temperature change of this magnitude, as well as changes in other key hydrometeorological variables, could have significant consequences for the thermal structure and also the aquatic ecology of the Great Lakes.

Although there is broad qualitative agreement among GCM's for monthly increases in air temperature in the Great Lakes region, the coefficients of variation among models for other predicted variables such as wind speed, humidity, and solar radiation are frequently large (Schertzer and Sawchuk 1990). Uncertainties in model predictions at the local scale are partially due to the spatial resolution of current GCM's (typically about 5° of latitude and longitude). This coarse grid resolution is sufficient to resolve large-scale processes, but the smaller (subgrid) processes must be parameterized. This dual aspect of model resolution and subgrid parameterization largely determines the model error (Gates 1985).

Preliminary analyses of climate warming impacts on the hydrological characteristics of the Great Lakes have been conducted for conditions of a doubling of atmospheric carbon dioxide. Cohen (1986) has investigated changes and sensitivites of water resources over the Great Lakes basin and suggested that under climate warming, net basin supplies could decrease significantly. Sanderson (1987) has indicated that flows in connecting channels of the Great Lakes may decrease approximately 20% due to changes in precipitation and evaporation. For Lake Erie, water levels may decrease by 60 cm or more, although downstream hydraulic controls would prevent such extreme changes in Lake Ontario. Cohen (1987) has indicated that air temperature and precipitation statistics from GCM's alone are not enough to completely assess the potential hydrological changes due to climate warming. For the Great Lakes, this necessitates the derivation of scenarios for other key components such as lake surface temperature and lake evaporation.

Schertzer and Sawchuk (1990) outlined some of the uncertainties in the GCM predictions and suggested that until the problem of increasing the spatial resolution of GCM predictions is solved, direct application of GCM predictions into regional scale models for simulation of heat fluxes, thermal structure, and water quality responses of lakes must be viewed with caution. Uncertainties in predictions for variables such as wind speed (reported as vector averaged winds) can give little confidence for computations of turbulent exchange components such as evaporation at the local scale. An alternative approach for assessing effects of climate warming on lake thermal responses is to examine components of the thermal regime during warmer than average years. This approach has only recently been exploited in climate change studies (e.g. Henderson-Sellers 1986) and ideally requires a long (e.g. 50–100 yr) series of observations or simulations. Unfortunately, such detailed observations are not available for Lake Ontario. Hansen and Lebedeff (1988) have determined that the four warmest years for global air temperatures in the period for which useful instrument data have been recorded occurred in the 1980's. The warmest years in order of decreasing temperature were 1981, 1987, 1980, and 1983. Figure 3a depicts heat contents for Lake Ontario for one of these years (1983) derived from lakewide vertical temperature observations at a grid of stations over the lake measured by NWRI. Clearly, heat content observed in 1983 shows that conditions in this warmer than average year were at the extreme maximum of observations, with largest increases in the lake heat storage occurring in the winter months. Detailed analysis of the meteorological conditions in 1983 for

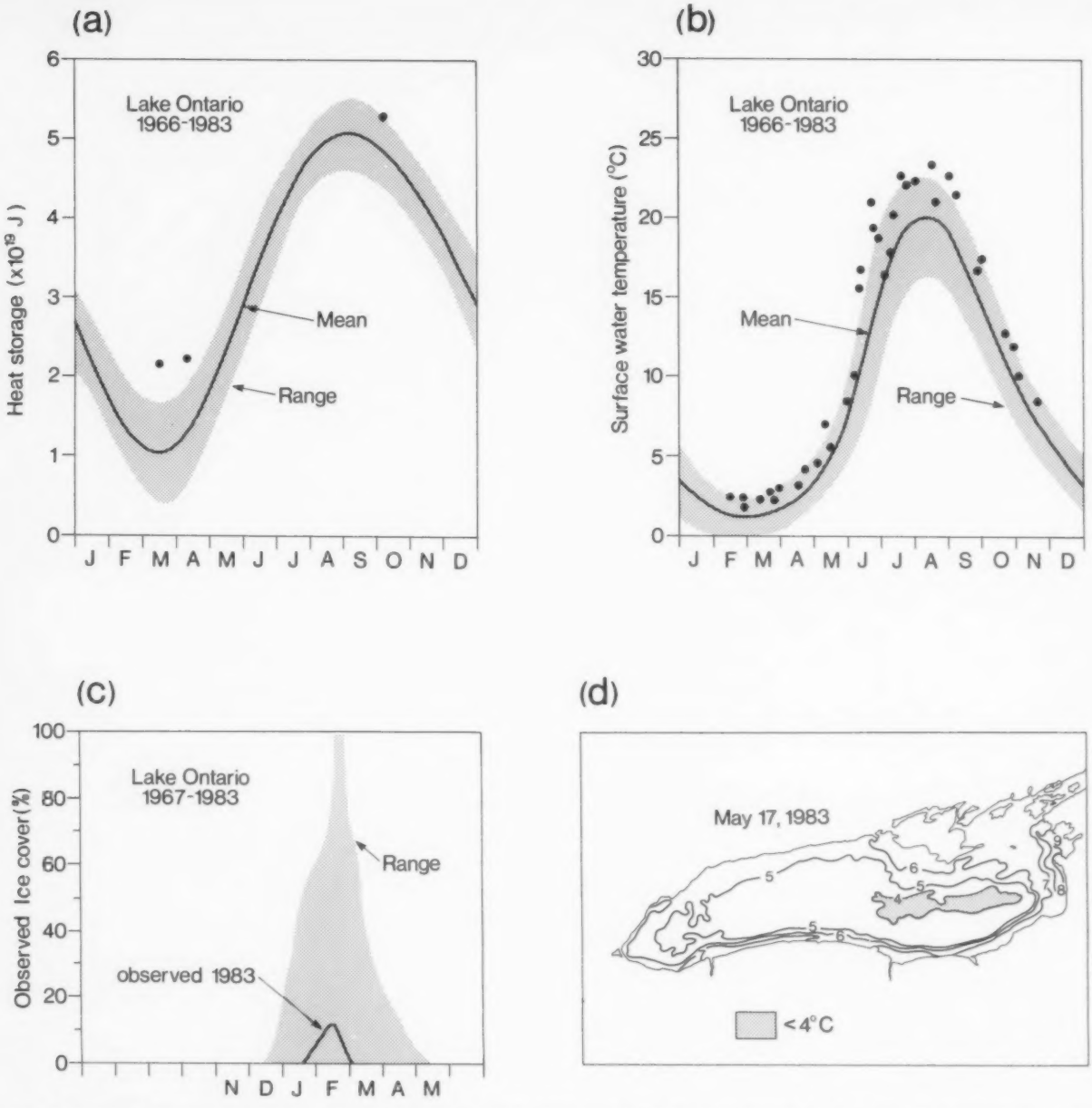


FIG. 3. Thermal characteristics of Lake Ontario for the anomalously warm year 1983. (a) Heat storage; (b) surface water temperature; (c) ice cover; (d) location of the 4°C isotherm. ●, 1983 measurements.

the lower Great Lakes (Lake Erie in particular) (Sawchuk and Schertzer 1988) revealed that 1983 wintertime (November 1982 to April 1983) showed air (and dewpoint) temperatures from 2 to 10°C above average, several intense cyclonic events largely responsible for warm air advection into the Great Lakes basin, lower than normal wind speeds, and substantially reduced surface heat fluxes contributing to the higher heat storage (Fig. 3a). During summer, air (and dewpoint) temperatures were 2–4°C above average, with conditions of high atmospheric pressures, reduced wind speeds, and reduced cloudiness. The extended anticyclonic conditions resulted in above-average surface heat fluxes (gains) which also contributed to higher water temperatures and heat storage in these months. The limitation in examining one year is that the selected year may itself be a transient response, and therefore not necessarily representative of an equilibrium steady-state climate resulting from, say, a doubling of atmospheric carbon dioxide concentrations. Consequently the examination of the lake thermal responses in a warmer than average year such as 1983 was considered as one possible sample of lake thermal response in a warmer climate.

The primary elements of the lake thermal response to seasonal gains and losses in lake heat content include surface water temperature, ice cover, formation of the thermal bar and disappearance of the 4°C isotherm, thermocline depth, and duration of the stratification period. Schertzer and Sawchuk (1990) examined these characteristics for Lake Ontario for 1983 to infer potential lake responses under climate warming conditions. Long-term observations (1966–83) of surface water temperature from lake surveillance (NWRI), airborne radiometer techniques, and satellite observations (Atmospheric Environment Service (AES) 1983) have established a mean temperature range from approximately 2°C (February) to 20°C (August). Figure 3b illustrates that in 1983, surface water temperatures were at maximum values recorded over this period throughout the year.

Ice cover is a function of surface water temperatures and prevailing meteorological conditions, primarily air temperatures (Assel et al. 1983). Figure 3c illustrates the long-term (1967–83) range in ice extent and duration over Lake Ontario. Normal ice cover is approximately 30%. The warmer than average conditions of 1983 indicate that the maximum ice extent achieved was only approximately 10% of the lake surface and the duration of ice cover was from mid-January to the beginning of March, being significantly less than other years.

The duration of the thermal bar in Lake Ontario appears also to be affected by warmer than average conditions. The length of time between onset and disappearance of the thermal bar is a complicated function of both the physical characteristics of the lake and prevailing meteorological conditions. In deeper Lake Ontario, the thermal bar usually persists until mid-June (Saylor et al. 1981). Satellite observations of surface water temperatures (AES 1983) during 1983 reveal that the 4°C isotherm had nearly disappeared between May 17 and May 24 in Lake Ontario (Fig. 3d). Rodgers (1987) examined the date of disappearance of the 4°C isotherm as a function of water temperature on April 1 in the top 100 m in the deepest basin of Lake Ontario. Measurements over the period 1967–83 not only indicated the anomalously warm conditions in 1983 associated with one of the most intense and longest lasting El Niño events on record (Ramage 1987), but also demonstrated that in years in which meteorological conditions do not favour extensive ice cover, available energy not required to melt ice can effect a much more rapid temperature increase and thus an earlier beginning to the summer stratification period (i.e. 2–3 wk based on observations in 1983). Schertzer and Sawchuk (1990) demonstrated that this was more significant in shallower Lake Erie.

Vertical temperature observations at a grid of stations over the lake taken during lakewide surveillance cruises can be used to derive lakewide average temperature profiles from which to determine characteristics of the lake thermal stratification (Schertzer et al. 1987). Due to time and cost constraints, such observations cannot be performed frequently, and consequently, models are used to simulate the thermal structure. Several models have been tested for the Great Lakes (Lam and Schertzer 1987; McCormick and Meadows 1988; Patterson and Hamblin 1988). Daily lakewide averaged vertical temperature profiles for 1983 were simulated (Schertzer and Sawchuk 1990) for Lake Ontario using a one-dimensional empirical diffusion model developed by Simons (1980b). Temperature simulations and observations for warm conditions of 1983 (Fig. 4) over the upper 60-m depth range indicate that weak thermal stratification began in early June. Stable thermal stratification was established by the end of June when the base of the warm epilimnion formed relatively high up in the water column. This structure persisted throughout July and August in response to high levels of surface heating and reduced vertical mixing due to lower than normal wind speeds. Thermal stratification has effectively ended by the end of October.

As indicated previously, the inferences which can be made from examination of lake responses in only one warmer than average year must be viewed with caution. Observations for 1983 anomalously warm conditions indicate that under the influence of meteorological conditions which persisted in 1983, higher lake temperatures and lake heat contents could occur with significantly reduced ice cover and extent, earlier disappearance of the thermal bar, earlier beginning of the thermal stratification period, shallower upper mixed layers, and a longer stratification season. One analysis of climate change (Schneider 1988) suggests that the frequency of warmer years (possibly such as 1983) will increase, while the frequency of colder years will decrease but not necessarily be eliminated from the climate record. How the lake thermal characteristics will respond under successive years of increased surface heating cannot be answered from an examination of a single year and emphasizes the importance of both short-term (i.e. daily) and long-term (i.e. decades) variations in fully assessing effects of climate warming on lakes such as Lake Ontario.

Conclusions

The presence of many overlapping and interacting scales of motion in large lakes is also reflected in a patchiness of the distribution of nonphysical variables. This must be allowed for in both the collection and interpretation of field data. The multiplicity of scales has important consequences for our ability to "predict" lake behaviour via numerical models as information about previous states is progressively lost in model-generated noise. In the past two decades, the general features of the circulation and mixing of Lake Ontario have been successfully delineated. However, site-specific studies of a climatological nature will still be required from time to time in areas of concern. Increasingly sophisticated models of lake thermal structure have been developed and they will be useful in assessing the potential impact of climate change, particularly in the matter of convective overturning. Despite the increasing sophistication based on better physical understanding, these models, like their predecessors, require empirical inputs. Improved measurement techniques make us hopeful that this empirical information may eventually be determined in the lake itself instead of artificial laboratory situations. The process of "sediment focusing," so strongly linked to the fate of many organic contaminants, is only recently amenable to in situ study with instruments that respect the natural time and space scales of resuspension and settling. The rates of gas and vapour transfer across the air–water interface are known to depend on the physical behaviour of this interface, and in particular on the surface wave field; these dependencies are being actively explored. Experience over many years has consistently shown that large-lake studies of chemical and biological processes are difficult, if not impossible, to interpret in the absence of an adequate base of concurrent physical measurements, one that respects both the scales of the site and those of the intrinsic variability.

To a casual reader it may seem that our understanding of the physical workings of large lakes such as Lake Ontario has improved so substantially over the past two decades that little research remains to be done. The attentive reader will have

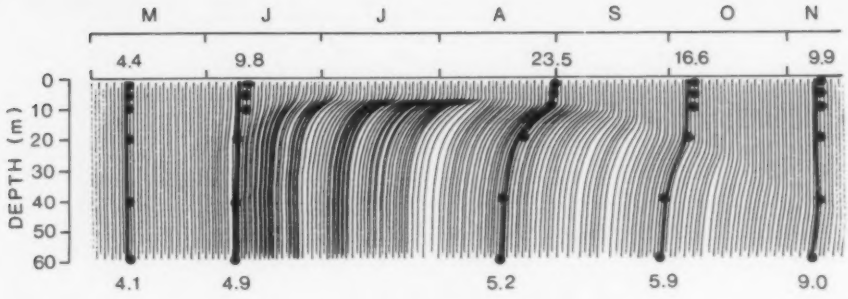


FIG. 4. Computed daily vertical temperature profiles (thin lines) for Lake Ontario from June to November 1983. Bold lines represent temperature profiles evaluated from Simons' (1980b) thermocline model; solid circles represent observed values from ship cruises, and dates shown are the midpoint dates of ship cruises. Numerical values represent observed temperatures.

noted, however, that while the general framework of our understanding has been strengthened, the structure requires cladding in many important places. A list of some of these research areas is included as an appendix to this paper. Because of the very large effort and expense required to obtain appropriate physical information, a multidisciplinary and multiinstitute "field year" approach has much to recommend it.

Acknowledgements

The authors wish to thank N. Rukavina, M. Skafel, M. Donelan, and A. Sawchuk for helpful comments. Constructive reviews and suggestions by K. M. Stewart and C. H. Mortimer are greatly appreciated.

References

ALLAN, R. J. 1986. The role of particulate matter on the fate of contaminants of aquatic ecosystems. IWD Sci. Ser. No. 142: 128 p.

ASSEL, R. A., F. A. QUINN, G. A. LESHKEVICH, AND S. J. BOLSENGA. 1983. Great Lakes ice atlas. Great Lakes Environmental Research Laboratory, Ann Arbor, MI.

ATMOSPHERIC ENVIRONMENT SERVICE (AES). 1983. Surface water temperatures for Lake Erie and Lake Ontario by satellite observation. Available from Hydrometeorology and Applications Division, Atmospheric Environment Service, Downsview, Ont. M3H 5T4.

AUBERT, E. J., AND T. L. RICHARDS [ED.] 1981. IFYGL: the international field year on the Great Lakes. National Oceanic and Atmospheric Agency, Great Lakes Environmental Research Laboratory, Ann Arbor, MI. 410 p.

BABA, N. 1974. A numerical investigation of Lake Ontario dynamics and thermodynamics. Ph.D. thesis, Princeton University, Princeton, NJ. 246 p.

BEDFORD, K. W., AND M. ABDELRHMAN. 1987. Analytical and experimental studies of the benthic boundary layer and their applicability to near bottom transport in Lake Erie. J. Great Lakes Res. 13: 628–648.

BEDFORD, K., R. VAN EVRA, AND C. MOORE. 1983. The measurement and analysis of wave affected sediment resuspension and vertical flux rates; Vol. 1: The development of microprocessor-based instrumentation for measuring the near-bottom momentum of sediment profile fields. USEPA Project Report. Large Lakes Research Station, Grosse Ile, MI.

BENNETT, J. R. 1971. Thermally driven lake currents during the spring and fall transition periods. Proc. 14th Conf. Great Lakes Res. Int. Assoc. Great Lakes Res. 533–544.

1974. On the dynamics of wind-driven lake currents. J. Phys. Oceanogr. 4: 400–414.

BLUMBERG, A. F. 1986. Turbulent mixing processes in lakes, reservoirs, and impoundments, p. 79–104. *In* W. G. Gray [ed.] Physics-based modelling of lakes, reservoirs, and impoundments. American Society of Civil Engineers, New York, NY. 308 p.

BOYCE, F. M., M. A. DONELAN, P. F. HAMBLIN, C. R. MURTHY, AND T. J. SIMONS. 1989. Thermal structure and circulation in the Great Lakes. Atmosphere-Ocean 27(4): 607–642.

CANADIAN CLIMATE CENTRE (CCC). 1986. Understanding CO_2 and climate — Annual report 1985. Atmospheric Environment Service, Environment Canada, Downsview, Ont. M3H 5T4. 23 p.

CHAMBERS, R. L., AND B. J. EADIE. 1981. Nepheloid and suspended particulate matter in southeastern Lake Michigan. Sedimentology 28: 439–447.

CHARLTON, M. N. 1980. Oxygen depletion in Lake Erie: has there been any change? Can. J. Fish. Aquat. Sci. 37: 72–81.

COHEN, S. J. 1986. Impacts of CO_2-induced climatic change on water resources in the Great Lakes basin. Clim. Change 8: 135–153.

1987. Sensitivity of water resources in the Great Lakes region to changes in temperature, precipitation, humidity and wind speed. Proc. of the Vancouver Symposium, August 1987, The Influence of Climate Change and Climatic Variability on the Hydrological regime and Water Resources. IAHS Publ. No. 168: 489–499.

COORDINATING COMMITTEE ON GREAT LAKES BASIC HYDRAULIC AND HYDROLOGIC DATA (CCHD). 1976. Lake Erie outflow 1860–1964 with addendum 1965–1975, Chicago, Illinois and Cornwall, Ontario, June 1976. 20 p.

CSANADY, G. T. 1970. Dispersal of effluents in the Great Lakes. Water Res. 4: 79–114.

1971. Coastal entrapment in Lake Huron. Proc. 5th International Water Pollution Conference. Pergamon Press, New York, NY.

1982. Circulation of the coastal ocean. D. Reidel Publishing Company, Dordrect, Holland. 279 p.

1984. Milestones of research on the physical limnology of the Great Lakes. J. Great Lakes Res. 10: 114–125.

DONELAN, M. A. 1989. Air–sea interaction. NWRI Contrib. 89–96: 128 p.

DUNCAN, G. A., AND G. G. LAHAIE. 1979. Size-analysis procedures used in the Sedimentology Laboratory, NWRI. NWRI Hydraul. Div. Man. 23 p.

FISCHER, H. B., E. J. LIST, R. C. Y. KOH, J. IMBERGER, AND N. H. BROOKS. 1979. Mixing in inland and coastal waters. Academic Press, New York, NY. 438 p.

GATES, W. L. 1985. The use of general circulation models in the analysis of the ecosystem impacts of climate change, Clim. Change 7: 267–284.

GORHAM, E., AND F. M. BOYCE. 1989. The influence of lake surface area and depth upon thermal stratification and the depth of the summer thermocline. J. Great Lakes Res. 15(2): 233–245.

HAMBLIN, P. F., R. C. HARRIS, AND W. J. SNODGRASS. 1987. Mixing in reservoirs, p. 627–644. *In* Proc. 8th Canadian Hydrotechnical Conference, Montreal, Canada, May 19–22/87. Canadian Society for Civil Engineering. 773 p.

HAMBLIN, P. F., J. A. BULL, AND F. CHIOCCHIO. 1989. A note on a microprocessor–based recording current meter modified for wave research. Ocean Eng. 16(5/6): 567–574.

HANSEN, J., D. JOHNSON, A. LACIS, S. LEBEDEFF, P. LEE, D. RIND, AND G. RUSSEL. 1981. Climate impact on increasing atmospheric carbon dioxide. Science (Wash., DC) 213: 957–966.

HANSEN, J., A. LACIS, D. RIND, G. RUSSEL, P. STONE, I. FUNG, R. RUEDY, AND J. LERNER. 1984. Climate sensitivity: analysis of feedback mechanisms, Climate processes and climate sensitivity. Maurice Ewing Series 5. American Geophysical Union, Washington, DC.

HANSEN, J., AND S. LEBEDEFF. 1988. Global surface air temperatures; Update through 1987. Geophys. Res. Lett. 15: 323–326.

HARLEMAN, D. R. F. 1986. Hydrothermal modelling of reservoirs in cold regions: status and research needs. Cold Regions Hydrology Symposium, American Water Resources Association, Fairbanks, AK. 3950 p.

HENDERSON-SELLERS, B. 1985. A new formulation of eddy diffusivity thermocline models. Appl. Math. Model. 9: 441–446.

HENDERSON-SELLERS, A. 1986. Increasing cloud in a warming world. Clim. Change 9: 267–309.

HOLLAN, E., P. F. HAMBLIN, AND H. LEHN. 1990. Long-term modelling of stratification in large lakes: application to Lake Constance, p. 107–124. *In* M. Tilzer and C. Serruya [ed.] Large lakes — Ecological structure and function. Springer-Verlag, New York, NY. 691 p.

IMBERGER, J., AND P. F. HAMBLIN. 1982. Dynamics of lakes, reservoirs, and cooling ponds. Annu. Rev. Fluid Mech. 14: 153–187.

IVEY, G. N., AND P. F. HAMBLIN. 1989. Convection near the temperature of maximum density for high Rayleigh number, low aspect ratio, rectangular cavities. J. Heat Transfer 3: 100–105.

IVEY, G. N., AND J. C. PATTERSON. 1984. A model of the vertical mixing in Lake Erie in summer. J. Limnol. Oceanogr. 29: 553–563.

LAM, D. C. L., C. R. MURTHY, AND R. B. SIMPSON. 1984. Effluent transport and diffusion models for the coastal zone. Springer-Verlag, New York, NY. 168 p.

LAM, D. C. L., AND W. M. SCHERTZER. 1987. Lake Erie thermocline model results: comparison with 1967–1982 data and relation to anoxic occurrences. J. Great Lakes Res. 13: 757–769.

LESHT, B. M., AND N. HAWLEY. 1987. Near bottom currents and suspended sediment concentration in southeastern Lake Michigan. J. Great Lakes Res. 13: 375–383.

LICK, W., AND S. W. KANG. 1987. Entrainment of sediments and dredged material in shallow water. J. Great Lakes Res. 13: 619–627.

LORENZ, E. N. 1969. The predictability of a flow which possesses many scales of motion. Tellus 21: 289–307.

MAAROUF, A. R. 1985. Carbon dioxide effects on climate with emphasis on climate model results for Canada. Available from Canadian Climate Centre, Canadian Atmospheric Environment Service, Downsview, Ont. M3H 5T4.

MCCORMICK, M. J., AND G. A. MEADOWS. 1988. An intercomparison of four mixed layer models in a shallow inland sea. J. Geophys. Res. 93(C6): 6774–6788.

MCCRIMMON, R. C., AND P. F. HAMBLIN. 1988. Numerical experiments on the gravitational collapse of stratified water columns including compressibility effects. NWRI Contrib. No. 88–33: 59 p.

MUDROCH, A. 1983. Distribution of major elements on sediment cores from western basin of Lake Ontario. J. Great Lakes Res. 9: 125–132.

MURTHY, C. R. 1972. Complex diffusion processes in coastal currents of a lake. J. Phys. Oceanogr. 2: 80–90.

MURTHY, C. R., T. J. SIMONS, AND D. C. L. LAM. 1986. Dynamics and transport modelling of the Niagara River plume in Lake Ontario. Rapp. P.-V. Réun. Cons. Int. Explor. Mer. 186: 150–164.

NATIONAL WATER RESEARCH INSTITUTE (NWRI). 1988. Collected reprints of Theodore Johannes Simons (1939–1987). W. M. Schertzer, F. M. Boyce, and C. R. Murthy [ed.] National Water Research Institute, Environment Canada, Burlington, Ont.

PATTERSON, J. C., AND P. F. HAMBLIN. 1988. Thermal simulation of a lake with winter ice cover. J. Limnol. Oceanogr. 33: 323–338.

POLLARD, R. T., P. B. RHINES, AND R. O. R. Y. THOMPSON. 1973. The deepening of the wind-mixed layer. Geophys. Fluid Dynam. 3: 381–404.

RAMAGE, C. S. 1987. Necessary and sufficient conditions for El Niño. *In* U. Radok [ed.] Toward understanding climate change. The J. O. Fletcher lectures on problems and prospects of climate analysis and forecasting. Westview Press, Boulder, Co. 200 p.

RODGERS, G. K. 1987. Time of onset of full thermal stratification in Lake Ontario in relation to temperatures in winter. Can. J. Fish. Aquat. Sci. 44: 2225–2229.

ROSA, F. 1985. Sedimentation and sediment resuspension in Lake Ontario. J. Great Lakes Res. 11: 13–25.

ROYER, L., F. CHIOCCHIO, AND F. M. BOYCE. 1987. Tracking short term physical and biological changes in the Central Basin of Lake Erie. J. Great Lakes Res. 13: 587–606.

RUKAVINA, N. A., AND A. J. ZEMAN. 1987. Erosion and sedimentation along a cohesive shoreline — the North-Central shore of Lake Erie. J. Great Lakes Res. 13: 202–217.

SANDERSON, M. A. 1987. Implications of climate change for navigation and power generation in the Great Lakes. *In* Climate change digest. Report. No. CCD 87–03. Atmospheric Environment Service, Downsview, Ont. 20 p.

SAWCHUK, A. M., AND W. M. SCHERTZER. 1988. Climatology of Lake Ontario and Lake Erie surface heat exchanges (1953–1983). NWRI Contrib. No. 88–37: 169 p.

SAYLOR, J. H., J. R. BENNET, F. M. BOYCE, P. C. LIU, C. R. MURTHY, R. L. PICKET, AND T. J. SIMONS. 1981. Water movements, p. 247–324. *In* E. J. Aubert and T. L. Richards [ed.] IFYGL — The International Field Year for the Great Lakes. Great Lakes Environmental Research Laboratory, Ann Arbor, MI.

SAYLOR, J. H., AND G. S. MILLER. 1988. Observation of Ekman veering at the bottom of Lake Michigan. J. Great Lakes Res. 14: 94–100.

SCHERTZER, W. M., AND A. M. SAWCHUK. 1990. Thermal structure of the Lower Great Lakes in a warm year: implication to occurrence of hypolimnion anoxia. Trans. Am. Fish. Soc. 119(2): 195–209.

SCHERTZER, W. M., J. H. SAYLOR, F. M. BOYCE, D. C. ROBERTSON, AND R. RESA. 1987. Seasonal thermal cycle of Lake Erie. J. Great Lakes Res. 13: 468–486.

SCHNEIDER, S. H. 1988. The green-house effect and the U.S. summer of 1988: cause and effect or a media event Clim. Change 13: 113–115.

SIMONS, T. J. 1974. Verification of numerical models of Lake Ontario: Part I: Circulation in spring and early summer. J. Phys Oceanogr. 4: 501–523.

1975. Verification of numerical models of Lake Ontario: Part II; Stratified circulations and temperature changes. J. Phys. Oceanogr. 5: 98–110.

1976. Verification of numerical models of Lake Ontario: Part III; Long term heat transport. J. Phys. Oceanogr. 6: 372–378.

1980a. Circulation models of lakes and inland seas. Can. Bull. Fish. Aquat. Sci. 203: 146 p.

1980b. Verification of seasonal stratification models. Available from Institute for Meteorology and Oceanography, University of Utrecht, The Netherlands. 12 p.

SIMONS, T. J., AND D. C. L. LAM. 1978. Nutrient exchange between volume elements of large lakes. *In* Modelling the water quality of the hydrological cycle — A Symposium. Proceedings of the Baden Symposium, 1978. IAHS/AISH Publ. No. 125.

1980. Some limitations of water quality models for large lakes. Water Resour. Res. 16: 105–116.

SIMONS, T. J., C. R. MURTHY, AND J. E. CAMPBELL. 1985. Winter circulation in Lake Ontario. J. Great Lakes Res. 11: 423–433.

SIMONS, T. J., AND W. M. SCHERTZER. 1986. Modelling wave-induced sediment resuspension in Lake St. Clair. NWRI Intern. Rep. 44 p.

1987. Stratification, currents, and upwelling in Lake Ontario, summer 1982. Can. J. Fish. Aquat. Sci. 44: 2047–2058.

SPIGEL, R. H., AND J. IMBERGER. 1980. The classification of mixed layer dynamics in lakes of small to medium size. J. Phys. Oceanogr. 10: 1104–1121.

STEPIEN, I., D. C. L. LAM, C. R. MURTHY, M. E. FOX, AND J. CAREY. 1987. Modelling of toxic contaminants in the Niagara River plume in Lake Ontario. J. Great Lakes Res. 13: 250–263.

STRACHAN, W. M. J., AND S. EISENREICH. 1987. Mass balance accounting of PCB's and lead in the aquatic environment, p. 1765–1770. *In* Proceedings: Oceans '87 Conference. Vol. 5: Coastal and Estuarine Pollution. Halifax, September. Available from IEE Service Centre, 445 Hoes Lane, Piscataway, NJ 08854.

SVENSSON, U. 1978. A mathematical model of the seasonal thermocline. Institute of Technology Report No. 1002. University of Lund, Sweden.

TAYLOR, W. D., H.-J. FRICKER, AND D. R. S. LEAN. 1987. Zooplankton seasonal succession in Lake Ontario at northshore, midlake, and southshore stations in 1982, and a comparison with 1970. Can. J. Fish. Aquat. Sci. 4: 2178–2184.

TENNEKES, H. 1988. The outlook: scattered showers. Bull. Am. Meteorol. Soc. 69: 368–372.

TSAI, C.-H., S. IACOBELLIS, AND W. LICK. 1987. Flocculation of fine-grained lake sediments due to a uniform shear stress. J. Great Lakes Res. 13: 135–146.

TSAI, C.-H., AND W. LICK. 1986. A portable device for measuring sediment resuspension. J. Great Lakes Res. 12: 314–321.

WEI, G. Y., AND P. F. HAMBLIN. 1986. Reservoir water quality simulations in cold regions, p. 167–177. *In* Cold Regions Hydrology Symposium. American Water Resources Association, Fairbanks, AK.

WHITE, D. S., P. C. KLAHR, AND J. A. ROBBINS. 1987. Effects of temperature and density of sediment reworking by *Styrodrilus heringianus* (Oligochatea; Lumbriculidae). J. Great Lakes Res. 13: 147–156.

ZILITINKEVICH, S. S., AND A. YU TERZHEVIK. 1987. The thermal bar. Oceanology 27: 549–554.

Appendix: Areas for Further Physical Research

(1) Better quantification of the relatively weak mixing processes in the hypolimnion.

(2) Better understanding of the general process of sediment focusing in large lakes through investigations of (a) the critical conditions for resuspension of cohesive or fine-grained sediments, (b) the conditions required for the disposition of fine-grained sediments, and (c) the possibility that the concentrations of suspended sediments may at times be large enough to initiate turbidity currents.

(3) Development, verification, and application of more physically based radiative transfer models suitable for assessment of the surface heat flux and lake thermal stratification responses under climate change.

(4) A program for monitoring thermal structure of large lakes to detect the effects of climate change.

(5) Systematic investigation of the potential impacts of climate change on ecosystem components and water quality using a combination of long time series data and updated atmospheric general circulation models.

(6) Improvements in algorithms for the extrapolation of land-based meteorological measurements to the adjacent lake surfaces and for extrapolation of GCM predictions to the local scale.

(7) A better observational base leading to improved simulations of small- to medium-scale processes in the nearshore zone, including lateral mixing, dynamics of the bottom boundary layer as related to sediment resuspension, upwellings, and downwellings.

(8) Observational base and model development for the transfer of heat, momentum, and materials across the air–water interface, taking into account the effects of breaking surface waves.

(9) Investigation of the spatial variability or "patchiness" of biochemical parameters as a result of physical and biochemical processes in order to define more rational sampling strategies for long-term monitoring.

Historical Nutrient Enrichment of Lake Ontario: Paleolimnological Evidence

Claire L. Schelske

Department of Fisheries and Aquaculture, University of Florida, 7922 NW 71st Street, Gainesville, FL 32606, USA

Schelske, C. L. 1991. Historical nutrient enrichment of Lake Ontario: paleolimnological evidence. Can. J. Fish. Aquat. Sci. 48: 1529–1538.

Recent studies of Lake Ontario show four periods of nutrient enrichment that can be identified from the sediment record in this phosphorus-limited system: pristine phosphorus loads (early 1800s before European settlement), moderate increase in phosphorus loading after settlement (beginning approximately 1850), exponential increase in phosphorus loading from urban sources (approximately 1940–70), and decreased phosphorus loading as the result of phosphorus abatement strategies (beginning in mid-1970s). Paleolimnological data are used to infer new paradigms about historical dynamics and cycling of major nutrients. The temporal pattern of organic carbon production closely parallels changes in phosphorus loading. Silica supplies which were replete for diatom production before forest clearance in the mid-1800s became limiting for diatom production in the summer epilimnion after 1865 and in the water column after 1950. Silica reserves were depleted by increased diatom production and sedimentation that resulted from increased phosphorus loading. Biologically induced precipitation of calcite began after 1940 as an indirect effect of increased urban phosphorus loading on primary productivity. Calcite began to be precipitated when historical increases in CO_2 utilized for primary productivity increased epilimnetic pH and the calcium carbonate saturation product was exceeded.

Des études récentes du lac Ontario montrent quatre périodes d'enrichissement des nutriments qui, dans ce système pauvre en phosphore, peuvent être identifiées à partir des sédiments : charges anciennes de phosphore (au début des années 1800, avant la colonisation européenne), accroissement modéré de la charge de phosphore après la colonisation (débutant vers 1850), croissance exponentielle de la charge de phosphore d'origine urbaine (approximativement entre 1940 et 1970) et diminution de la charge de phosphore causée par suite de l'application des stratégies de réduction du phosphore (les ni-années 70). À l'aide de données paléolimnologiques, on propose de nouveaux modèles de la dynamique évolutive et du recyclage des principaux nutriments. Le modèle temporel de la production de carbone organique épouse étroitement les modifications de la charge de phosphore. Les réserves de silice qui, avant l'éclaircissement des forêts, étaient abondantes pour la production de diatomées, sont devenues un facteur limitant dans la production des diatomées dans l'épilimnion d'été après 1865, et dans la colonne d'eau après 1950. Les réserves de silice ont été épuisées par suite de l'accroissement de la production de diatomées et de la sédimentation causées par une augmentation de la charge de phosphore. La précipitation biologique de la calcite a débuté après 1940 et est un effet indirect de la charge accrue de phosphore d'origine urbaine sur la productivité primaire. La précipitation de la calcite a commencé au moment où les augmentations historiques du CO_2 utilisé pour la productivité primaire ont élevé le pH de l'épilimnion et où l'indice de saturation du carbonate de calcium a été dépassé.

Received January 24, 1989
Accepted February 5, 1990
(JA031)

Reçu le 24 janvier 1989
Accepté le 5 février 1990

Little is known about the early trophic history of Lake Ontario because few comprehensive studies were undertaken prior to 1964 (see Stevens and Neilson 1987). Studies prior to 1964 were based on isolated data collections and on data collected at nearshore sites, primarily at water treatment plants. The classic work by Beeton (1965) on the historical increase in conservative ions, which closely parallels the inferred trophic history, was based on a judicious and systematic analysis of these early data. Little is known about the biological responses that have occurred as the result of increased anthropogenic nutrient and conservative ion loading (see Beeton 1969; Stevens and Neilson 1987). Phosphorus data from comprehensive lake-wide surveys of this phosphorus-limited lake (see Schelske et al. 1986b; Lean et al. 1987) are only available beginning in 1964 (Stevens and Neilson 1987). Because historical information is limited, Chapra (1977) used simulation modelling to estimate phosphorus loading to Lake Ontario from 1800 to 1970.

Given the lack of historical data on either nutrients or trophic responses to increased nutrient loading, paleolimnological studies have been used to make inferences about nutrient loading and on biogeochemical and trophic responses to increased nutrient loading. Early eutrophication of the lower Great Lakes in the mid-1800s as a result of European settlement was inferred from chemical and microfossil analyses (Harris and Vollenweider 1982; Schelske et al. 1983, 1986a, 1988; Stoermer et al. 1985a, 1985b, 1987, 1989). Even earlier effects of nutrient enrichment during French settlement from 1669 to 1784 have been reported for the Bay of Quinte, Lake Ontario (Warwick 1980; Stoermer et al. 1985c; Schelske et al. 1985). These paleolimnological papers, published in the 1980s, reported major changes in biogeochemistry of nutrients and in phytoplankton community structure in the lower lakes after European settlement.

This surge in paleolimnological papers and inferences about relatively recent events in the paleorecord have been possible

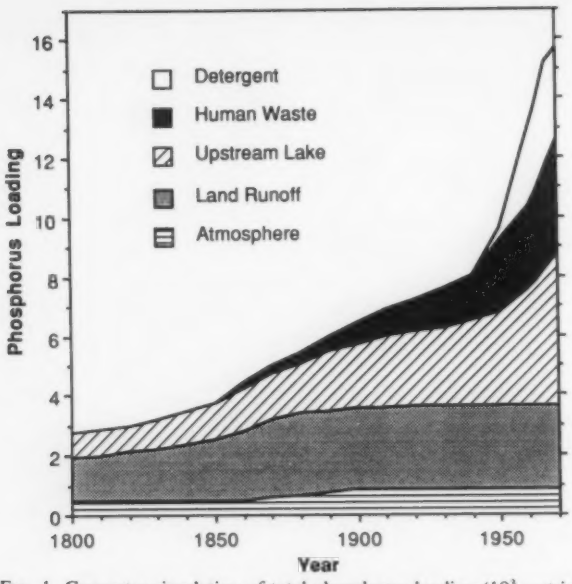


FIG. 1. Computer simulation of total phosphorus loading (10^3 metric tons·yr^{-1}) from 1800 to 1970 for Lake Ontario (from Chapra 1977).

for several reasons: (1) age estimates in recent sediments can now be obtained routinely using ^{210}Pb techniques, (2) accumulation rates of sediments and nutrients can be calculated from these age estimates, (3) better time resolution has been obtained as techniques have become available to sample finer intervals in cores, and (4) knowledge of depositional basins has provided locations of high sedimentation areas which have the best potential for coring.

High sedimentation areas with good coring sites for paleolimnological studies have been identified in the Rochester Basin in eastern Lake Ontario. It has been estimated that from 65% (Kemp and Harper 1976) to 80% (Thomas et al. 1972) of the fine-grained sediments are deposited in this basin. In this paper, data on nutrients and microfossils from cores collected in the Rochester Basin will be used to show that (1) Lake Ontario responded to increased phosphorus loading beginning with early European settlement and forest clearance in the mid-1800s, (2) major changes in the biogeochemistry of silica and carbon and in community structure of diatoms resulted from nutrient enrichment, and (3) new paradigms for major nutrients can be inferred from paleolimnological results. In addition, the importance of paleolimnological techniques in future studies of lake processes will be discussed.

Biogeochemical Responses to Nutrient Enrichment

Simulation modelling by Chapra (1977) shows two positive inflections in total phosphorus loading since 1800 (Fig. 1) and provides a basis to infer historical effects of nutrient enrichment in Lake Ontario. The first inflection beginning about 1850 simulates increased loading from land runoff and erosion after forest clearance during early settlement by Europeans. The second inflection, an exponential increase in phosphorus loading beginning in the late 1940s and extending over three decades, simulates introduction of phosphate-based detergents in combination with an increasing population being served by domestic sewer systems. Modelling results also show that Lake Erie,

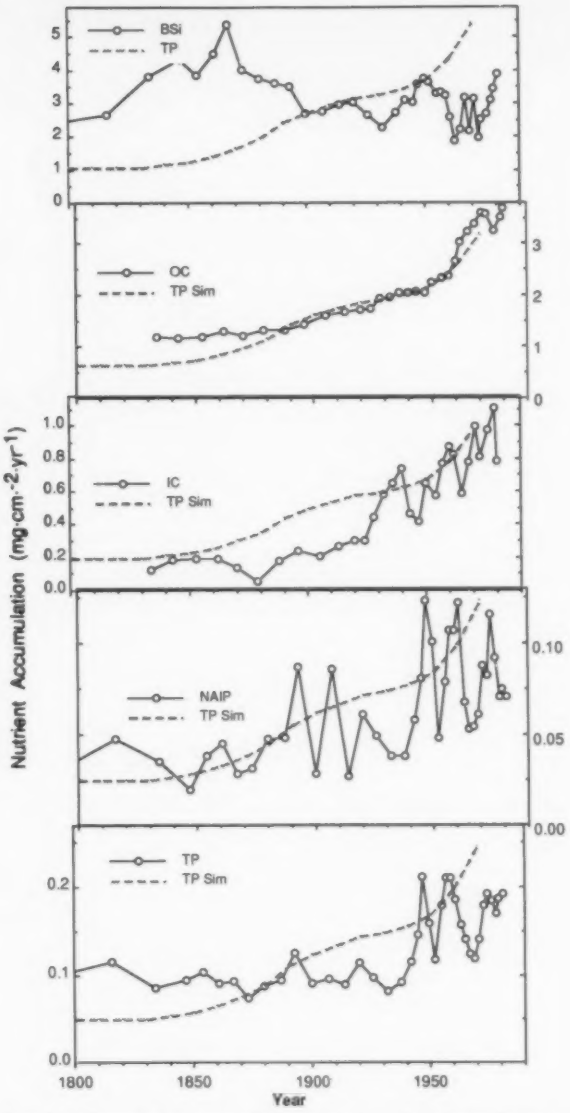


FIG. 2. Accumulation rates of biogenic silica (BSi), organic carbon (OC), inorganic carbon (IC), available phosphorus (NAIP), and total phosphorus (TP) in cores collected in 1981 at Station G32, Rochester Basin in eastern Lake Ontario (from Schelske et al. 1988), compared with computer simulation (broken line) of total phosphorus loading (from Chapra 1977) shown on a relative scale.

the upstream lake, contributes roughly one third of the loading. Positive inflections in loading from each source for the upstream lake, however, essentially follow the pattern shown for Lake Ontario (Chapra 1977).

Sedimentation of phosphorus was modelled on an annual basis as a proportion of total phosphorus in the water column (Chapra 1977). As a result, temporal patterns for modelled phosphorus loading (Fig. 1), total phosphorus concentration, and total phosphorus sedimentation would be identical. Trends in measured accumulation of total phosphorus differed substantially from the pattern obtained from modelling (Fig. 2) whereas general trends in NAIP (biologically available phos-

phorus) approximated modelled total phosphorus in this core but not in a second core studied by Schelske et al. (1988). This lack of coherence between measured accumulation and modelled losses of phosphorus was also found in other paleolimnological studies on the Great Lakes (see Schelske et al. 1986a, 1988; Kemp et al. 1972). Accumulation rates of both forms of phosphorus fluctuated widely over short time periods. Fluctuations resulted largely from variations in rates of accumulation of biologicaly available phosphorus.

Trends in accumulation rates of other nutrients in cores, however, have been attributed to phytoplankton responses to increases in phosphorus loading since the mid-1800s (Schelske et al. 1988). The earliest major response was an increase in biogenic silica accumulation that peaked in response to increased phosphorus loading from early settlement and forest clearance (Fig. 2). The peak in biogenic silica accumulation was attributed to increased production of phosphorus-limited diatoms and the subsequent decrease in diatom production when epilimnetic silica reserves were depleted (Schelske et al. 1983). According to ^{210}Pb age estimates of sediments, this peak occurred about 1865 (Schelske et al. 1988). A less distinct peak in biogenic silica accumulation occurred after 1940. This minor peak was hypothesized to have resulted from the exponential increase in phosphorus loading from urban sources (see Schelske et al. 1986b). The resulting increased phosphorus supplies increased diatom production during the winter–spring mixing period to the extent that silica supplies over the entire water column became limiting for diatom production. This effect of increased urban phosphorus loading, defined as severe silica limitation, produced an environment in which diatom production was silica limited during most of the annual production cycle (Schelske et al. 1986b).

The rate of carbon accumulation also increased as a biological response to increased phosphorus loading (Schelske et al. 1988). Organic carbon accumulation increased in two phases; a moderate increase began about 1850 after early European settlement, but the major increase occurred after 1940 when phosphorus loading from urban sources increased exponentially (Fig. 2). Organic carbon accumulation closely paralleled the temporal pattern for modelled total phosphorus loading. Inorganic carbon accumulation increased rapidly after 1940 when increased photosynthetic uptake of CO_2 raised pH to the extent that the calcium carbonate solubility product was exceeded and calcium carbonate (calcite) was precipitated. The increase in biologically induced precipitation of calcite resulting from increased phytoplankton production was, therefore, a secondary response to nutrient enrichment (Kelts and Hsu 1978). Similar temporal patterns in organic carbon and calcite accumulation also were reported for a core collected from the Rochester Basin by Kemp et al. (1972).

Paleolimnological results reviewed here show that the biogeochemistry of nutrients in Lake Ontario changed dramatically several times in less than 150 yr. Major changes in the biogeochemistry of silica and inorganic carbon occurred within one or two decades. These changes are attributable either directly or indirectly to increased primary production in the lake. Increases in organic carbon and biogenic silica can be attributed directly to increased primary production whereas increases in calcite were biologically induced by increased primary production. Overall these biogenic components increased the calculated mass sedimentation rate in recent sediments by as much as 25% in comparison with the mid-1800s (Schelske et al. 1988).

Ecological changes in primary production and primary producers over the past 200 yr were inferred from paleolimnological analysis of siliceous microfossils and related to increased nutrient loading (Stoermer et al. 1985a). One conclusion was that the phytoplankton community was severely modified soon after early European settlement in the drainage basin, before major modifications occurred at higher trophic levels. Changes in community structure and abundance were associated with the two positive inflections in modelled phosphorus loading, first from forest clearance and later from the exponential increase in urban phosphorus loading (Fig. 1). Results thus support the importance of phosphorus as a controlling factor for historical changes in phytoplankton production and community structure.

Microfossil results, like those of biogenic silica, support the conclusion that two stages of silica limitation for diatom growth have occurred since 1850 (Stoermer et al. 1985a). The initiation of epilimnetic silica depletion, the first stage, is marked by an increase in biogenic silica accumulation that peaked in 1865 (Fig. 2) and by the first major increase in summer blooming diatom species such as *Cyclotella comensis* and *C. stelligera*. Microfossil data indicate that severe silica depletion probably began after 1950 when there was a decrease in total planktonic diatoms and an increasing proportion of benthic, meroplanktonic, and nearshore species preserved in the core (Stoermer et al. 1985a). The high proportion of such species, which now grow mainly in nearshore and other areas with relatively high silica supplies (see Neilson and Stevens 1987), indicates that after 1950, diatom production in offshore waters of the lake was silica limited during most of the annual production cycle.

Paleolimnological analyses of a core from the Bay of Quinte also provide additional evidence that phosphorus enrichment affected the production dynamics of phytoplankton. Increases in biogenic silica accumulation indicate that the system was affected by nutrient enrichment in the period of French settlement from 1669 to 1784 (Fig. 3). This early effect when human population was low points to the extreme sensitivity of pristine phytoplankton assemblages to nutrient enrichment. The community structure of siliceous microfossil assemblages at this time was characterized by a high proportion of benthic and epiphytic species which indicates relatively high water transparency (Stoermer et al. 1985c). The change in siliceous microfossil communities after large-scale forest clearing in the early 1850s to those dominated by planktonic species indicates reduced water clarity. This change would be expected with nutrient enrichment if the increase in phytoplankton standing crop shades the benthic plant community (Stoermer et al. 1985c).

Coincident increases in phosphorus and biogenic silica accumulation during this period of forest clearance in the Bay of Quinte watershed indicate that increased phosphorus loading increased diatom production and that the system was phosphorus limited (Fig. 3). Rates of biogenic silica accumulation after 1890 (Zones VIII and IX) were maintained at a high level relative to total phosphorus accumulation. These high rates of biogenic silica accumulation most likely resulted from an increase in diatom production stimulated by an increasing proportion of available phosphorus in phosphorus loads. An increase in available phosphorus at this time has been attributed to construction of sewage collection systems (Schelske et al. 1985). This increase in supplies of available phosphorus may have produced an environment characterized by severe silica limitation (see Schelske et al. 1986b). Under such conditions, soluble silica inputs from the watershed would be utilized primarily for

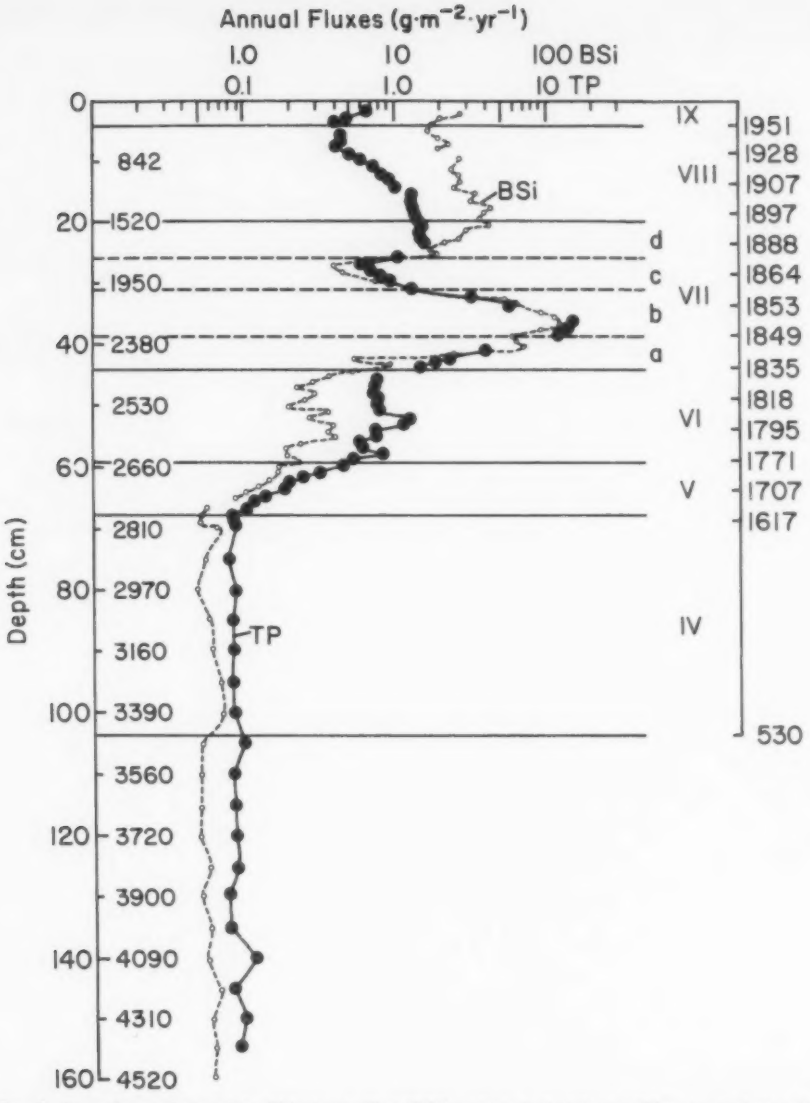


FIG. 3. Annual rate (log scale) of biogenic silica (BSi) and total phosphorus (TP) accumulation in the Glenora-B core, Bay of Quinte (from Schelske et al. 1985). Zones and dates listed on the right side of the figure are those given by Warwick (1980). Numbers on the left side of the figure represent the cumulative inventory of biogenic silica ($g \cdot m^{-2}$) to specific depths.

diatom production and be sedimented in the bay. The inventory of biogenic silica in the Bay of Quinte core supports this conclusion in that roughly one third of the total inventory in the 2800-yr core was deposited after 1890.

New Nutrient Paradigms

In the absence of long-term historical data collected from the water column, studies of the paleorecord provide a means to infer historical nutrient dynamics and changes. Much of the work reviewed here is based on studies of two cores collected in 1981 at Stations E30 and G32. Although the stations are only 25 km apart, the sedimentation rate at G32 is 2.24 times greater than at E30 (Schelske et al. 1988). Data from Station G32 with the higher sedimentation rate are used here because the resolution of events is much better than for E30.

Using data from these cores has two disadvantages: (1) they were collected in 1981, too soon after phosphorus abatement strategies were implemented in the mid-1970s to provide records of resulting system changes, and (2) they were sectioned too coarsely, except in the top 20 cm, to resolve the finer details of nutrient stratigraphy.

Phosphorus

The temporal pattern of total phosphorus accumulation in the sediment record (Fig. 2) differs markedly from the temporal pattern of total phosphorus loading modelled by Chapra (1977).

Measured total phosphorus differed by being higher from 1800 to 1870 and by being relatively constant from 1870 to 1940 than that simulated by modelling. A better fit might be expected because sedimentation of total phosphorus was modeled as a constant proportion of total phosphorus loading. These results suggest that total phosphorus loads prior to the 1940s were overestimated relative to the 1970 load.

To interpret this apparent discrepancy, the relative importance of different sources of increased phosphorus loading since 1800 should be considered (Fig. 1). The doubling in phosphorus loading from 1850 to 1900 was mainly from land runoff whereas the doubling in loading from 1940 to 1970 was mainly from urban sources. The increase in absolute loading from forest clearance, therefore, was small compared with that from detergents and sewage. In fact, in 1970, phosphorus from human wastes and detergents accounted for nearly 50% of the total loading and 67% of the in-lake loadings (when the contribution from upstream lakes is excluded). The relative changes in total phosphorus loading resulting from forest clearance and urban sources do not reflect the biological importance of the different sources. A much greater proportion of the phosphorus in human wastes and detergents is biologically available than in phosphorus from land runoff (see Schelske et al. 1988).

Chapra (1977) modelled changes in historical loading using uniform values for model parameters for each drainage basin. Loading to Lake Ontario from land runoff for forested land was 20 $kg \cdot km^{-2} \cdot yr^{-1}$ which increased to 40 $kg \cdot km^{-2} \cdot yr^{-1}$ when cleared for agricultural use and to 150 $kg \cdot km^{-2} \cdot yr^{-1}$ when cleared for urban use. Loading from richer agricultural land in the American drainage basin of western Lake Erie was greater, 100 $kg \cdot km^{-2} \cdot yr^{-1}$. Urban loads were based on 0.5 $kg \cdot capita^{-1} \cdot yr^{-1}$ for population in urban areas with a series of additional assumptions about effects of sewage treatment. Chapra (1977) noted that calculations based on lake basins may introduce a source of error because the resulting estimates from the model make no distinction between phosphorus that originates far from or in close proximity to the lake. It must be pointed out, however, that the data for more refined estimates do not exist for the large drainage basins of the Laurentian Great Lakes.

Assumptions by Chapra (1977) about the increase in phosphorus loading from land runoff may have contributed to the discrepancy in measured accumulation and modelled losses of total phosphorus. Bilby (1981) has shown that phosphorus trapped in the sediments and by debris dams of forested streams is a major source of phosphorus loading after forest clearance. Loading from these sources of phosphorus, however, does not continue at a uniform level after forest clearance. Within a few years after forest clearance, breakdown of debris dams and erosion of soil would decrease (Hedin et al. 1988) and the associated loading of phosphorus would be reduced, but probably not to preclearance levels. This type of pulsed loading of phosphorus has been documented for one drainage basin of Lake Ontario (Fig. 3).

An alternative hypothesis to account for the difference between measured accumulation rates of total phosphorus and Chapra's (1977) modelled phosphorus loads and concentrations, therefore, is the pulse model (Fig. 4). Instead of modelling phosphorus loading from land runoff as a constant over time after forest clearance, this qualitative inference model invokes a burst of phosphorus loading after forest clearing when erosion of cleared land, burning of forest debris, and break down of debris dams in streams would have been greatest. The hypothesized pulse of loading to the lake may not have been as sharp as shown in Fig. 4 because pulsed loading from individual drainage basins would have been spread over the period of most intensive forest clearance for the entire drainage basin. Some form of pulse loading, however, now appears to be the most reasonable simulation of mid- and late-1800s phosphorus loading.

How great a discrepancy exists between measured accumulation and present modelled losses of total phosphorus is not known. Estimating basin-wide sedimentation of phosphorus and other nutrients is complicated by effects of sediment focusing and possibly by differential focusing of nutrients in depositional basins (see Schelske et al. 1988). Nutrients other than biologically available phosphorus were stored in proportion to mass sedimentation rate in cores from two stations (Table 1). When normalized to mass sedimentation rate, about 50% more biologically available phosphorus was stored in core G32 than in core E30. Schelske et al. (1988) stated that additional cores must be collected to account for variability among cores so that reliable, basin-wide estimates of phosphorus losses can be calculated. To date, no direct estimates of basin-wide phosphorus losses to the sediments have been obtained.

Biological factors as well as physical-chemical factors may have affected how much phosphorus was deposited in the sediment over the past 150 yr (Schelske et al. 1988). For example, the qualitative character of primary producers changed in several stages after forest clearance (Stoermer et al. 1985a). Diatom production and sedimentation must have peaked shortly after forest clearance and now, due to silica limitation, may be comparable with pristine levels (Fig. 2), especially if the upper samples in the core were obtained from the dissolution zone which is not part of the permanent sediment record (Schelske et al. 1983). A large proportion of the diatom production now occurs during the winter–spring mixing period. Diatoms are sedimented, presumably along with nutrients such as phosphorus, as one of the major food sources for the amphipod *Pontoporeia hoyi* (Gardner et al. 1985). Before diatom production was silica limited, it was phased more uniformly over the annual cycle. In contrast with winter–spring production, summer epilimnetic production is grazed mainly by zooplankton which produce diffuse fecal material of which little is sedimented (Scavia and Fahnenstiel 1987; Lean et al. 1987).

The physical–chemical environment was altered in the last four decades by increased calcite precipitation (Fig. 2). Little soluble phosphorus appears to be coprecipitated with calcite in Lake Ontario because precipitation occurs late in the summer when soluble phosphorus levels are minimal (Lean et al. 1987). Particulate phosphorus, however, under some conditions may be precipitated with calcite or adsorbed on calcite surfaces (see Raidt and Koschel 1988). Historical changes in any of these factors could have altered the sedimentation coefficient of phosphorus, which was modelled as being constant over time (Chapra 1977), and contributed to the discrepancy between modelled and measured losses of phosphorus.

What was the total phosphorus concentration in pristine waters of Lake Ontario? Pristine levels are not known, but 5–6 $\mu g\ P \cdot L^{-1}$ was used for simulation modelling (Chapra 1977). Until the last few years such low levels, only slightly higher than present levels for Lake Huron or Lake Superior, appeared to be much too low. Phosphorus abatement measures initiated in the drainage basin in the 1970s, however, have produced substantial reductions in spring total phosphorus in Lake Ontario. Levels have been halved since the mid-1970s; spring

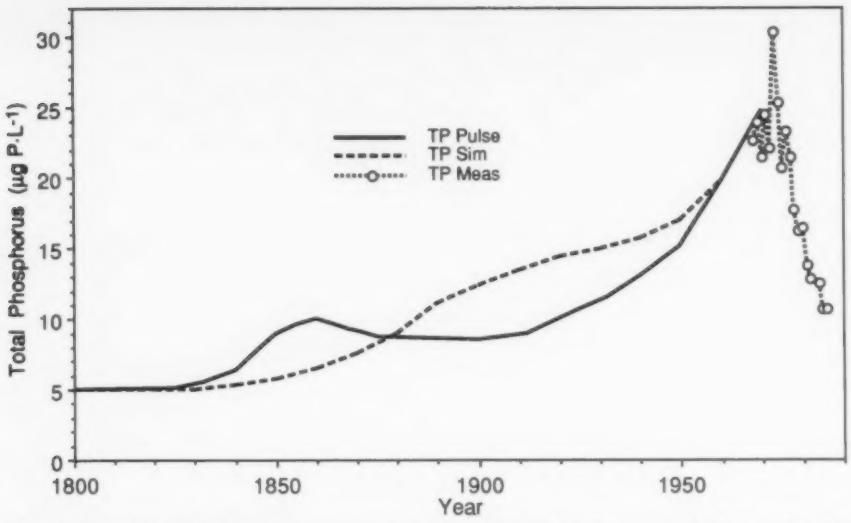


FIG. 4. Historical total phosphorus concentrations in Lake Ontario. Computer simulations (TP Sim) from 1800 to 1970 (Chapra (1977) and measured concentrations (TP Meas) during spring mixing from 1968 to 1982 (Stevens and Neilson 1987), 1984 (by author), and 1985 (International Joint Commission 1988). Hypothetical model based on pulsed loading (TP Pulse) from forest clearance (see text).

TABLE 1. Cumulative inventories ($mg \cdot cm^{-2}$) of nutrients to dates shown for cores collected from the Rochester Basin of Lake Ontario (Schelske et al. 1988). See Fig. 2 for data.

Date	Organic carbon	Inorganic carbon	Biogenic silica	Total phosphorus	Available phosphorus
			E30-RNB-81		
1950	48.7	17.3	28.6	1.99	0.719
1900	92.7	26.1	65.9	4.12	1.23
1850	128	27.7	158	6.35	2.17
1800	159	29.5	221	9.26	3.78
1750	191	30.1	263	11.6	4.93
1700	221	31.2	310	13.8	5.82
			G32-81		
1950	105	31.8	72.5	4.39	2.16
1900	220	61.0	212	9.75	4.85
1850	300	70.1	390	14.2	7.22
1800	—	—	564	18.8	8.94
1750	—	—	682	23.2	10.1
1700	—	—	839	27.4	11.7
G32/E30[a]	2.34	2.53	2.47	2.24	3.33

[a]Ratio of cumulative inventories to 1850.

total phosphorus decreased from an average of approximately 25 µg $P \cdot L^{-1}$ in the mid-1970s to 12.5 µg $P \cdot L^{-1}$ in 1982 (Stevens and Neilson 1987) and 10.7 µg $P \cdot L^{-1}$ by 1985 (International Joint Commission 1988). Paleolimnological results suggest that pristine phytoplankton assemblages responded to small increments in phosphorus loading and that the presettlement assemblage in Lake Ontario was similar to assemblages in Lake Superior (Stoermer et al. 1985a). These data and the assumption that present phosphorus loadings must be greater than pristine loadings indicate that the total phosphorus concentration in pristine Lake Ontario may have been comparable with present levels in Lake Huron or Lake Superior.

In summary, four periods in the trophic history of Lake Ontario can be identified from the sediment record and have been inferred to have resulted from historical changes in phosphorus loading (Fig. 5). During the presettlement period, total phosphorus concentrations were low, probably 5–6 µg $P \cdot L^{-1}$ according to Chapra (1977), or similar to concentrations now found in Lake Superior and Lake Huron. A prolonged pulse in phosphorus loading after forest clearance probably increased total phosphorus levels very little, possibly to 8–10 µg $P \cdot L^{-1}$ (Schelske et al. 1983, 1986b). Loadings to Lake Ontario during the postsettlement period probably decreased at some point and did not increase until loadings from urban development became important in the late 1800s and early 1900s (Chapra 1977). The largest increases in urban phosphorus loading, however, occurred over three decades (Chapra 1977) and increased phosphorus concentrations to more than 20 µg $P \cdot L^{-1}$ (Fig. 4). Urban loads decreased in the mid-1970s when phosphorus abatement practices became effective (Stevens and Neilson 1987).

Silica

Historical phasing of the stages of silica limitation for diatom production have been postulated from microfossil and biogeochemical studies of the sediment record (Fig. 5). Prior to settlement and forest clearance by Europeans in the mid-1800s, silica reserves in the waters of Lake Ontario were replete for diatom growth. Two stages of silica limitation for diatom growth occurred after settlement and forest clearance. Epilimnetic silica depletion, the first stage, occurred after 1865 when increases in diatom production and sedimentation that resulted from increased phosphorus loading from forest clearance depleted epilimnetic silica reserves. This increase in summer production of diatoms coupled with decreased supplies of silica from Lake Erie, the upstream lake, apparently decreased epi-

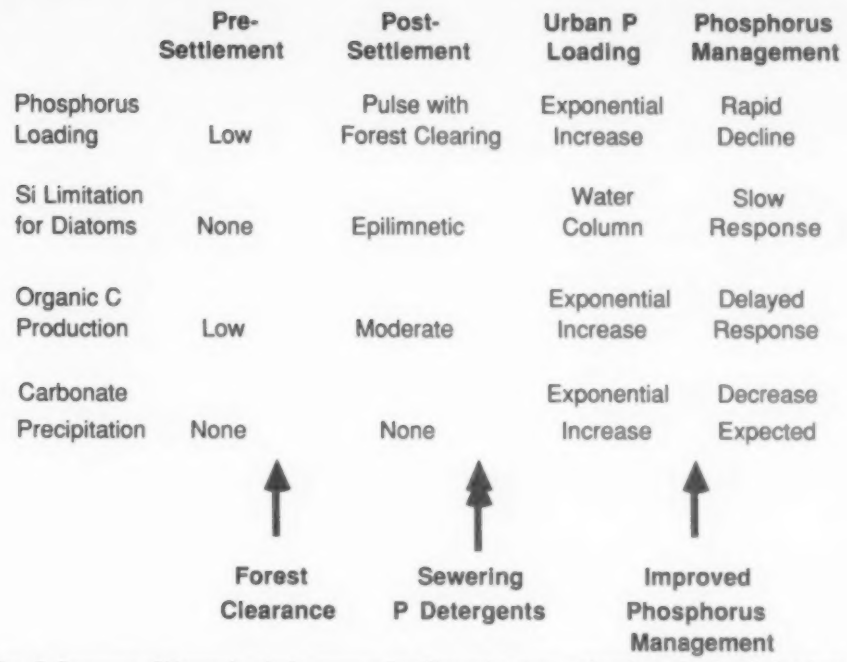


FIG. 5. Summary of biogeochemical responses for silica and carbon to phosphorus loading during four periods that have been identified in the sediment record. Settlement and extensive forest clearance by Europeans began in the mid-1800s, expansion of sewer systems and introduction of phosphate-based detergents began in the 1940s, and phosphorus abatement was instituted beginning in the early 1970s (see text).

limnetic silica reserves and resulted in rapid epilimnetic silica limitation, possibly within 10 or 20 yr (Schelske et al. 1983).

Severe silica depletion, the second stage, defined as the stage in which water column silica concentrations are <0.40 mg $SiO_2 \cdot L^{-1}$, characterizes Lake Ontario at the present time (Schelske et al. 1986b). In the 1970s and early 1980s, silica concentrations were no more than 0.5 mg $SiO_2 \cdot L^{-1}$ at the annual maximum and were reduced to as low as 0.1 mg $SiO_2 \cdot L^{-1}$ over most of the water column by the onset of thermal stratification (Dobson 1984; Lean et al. 1987). These low silica concentrations which would limit the growth of many diatom species probably have occurred since the 1950s (Stoermer et al. 1985a; Schelske et al. 1986b).

How much silica concentrations have changed historically is not known from water column sampling. Historically, silica concentrations in Lake Ontario must have been affected to some degree by upstream inputs because approximately 80% of the hydrologic input is from Lake Erie which receives more than 80% of its hydrologic inputs from upstream sources. The silica reservoir in Lake Ontario woud have been influenced by the silica concentration in other upstream lakes including Lake Michigan which historically had the highest silica concentration in the Great Lakes (Schelske et al. 1983). In the early 1900s, the winter maximum silica concentration in Lake Michigan may have been 4.5 mg $SiO_2 \cdot L^{-1}$ or possibly even larger (Schelske 1988). This threefold greater concentration than at present would have provided larger upstream inputs of silica to Lake Ontario through the outflow from Lake Michigan, first to Lake Huron and then to Lake Erie and Lake Ontario. The average silica concentration in Lake Huron was 2.3 mg $SiO_2 \cdot L^{-1}$ in the early 1960s and decreased to 1.5 mg $SiO_2 \cdot L^{-1}$ in the late 1970s (Schelske et al. 1983). Even greater silica concentrations would have been expected in Lake Huron in the early 1940s before the period of rapid silica depletion in the 1950s and 1960s in Lake Michigan (Schelske 1988). Silica inputs from Lake Michigan to Lake Huron in the mid-1800s up to the 1940s, therefore, would have been several times larger than at present.

Silica utilized for diatom production would be expected to decrease in response to decreased phosphorus loading and the resulting lower phosphorus concentration in the water (Schelske et al. 1986b). As a result the silica concentration in Lake Ontario might be expected to increase in response to the recent decrease in phosphorus concentration in lake water (Fig. 4). The response to phosphorus reduction, however, will be slow (Fig. 5) because the upstream input of silica from Lake Erie is very low. Chapra's (1977) simulation modelling has shown the importance of upstream loading for Lake Ontario (Fig. 1). In the case of silica, however, relatively little loading would be obtained from human waste and detergents. Inputs of silica from Lake Erie will be insufficient to supply Lake Ontario's needs until the silica demand for diatom production in Lake Erie is reduced substantially. In addition, because Lake Ontario and Lake Erie have been characterized by severe silica depletion, silica demand for diatom production has exceeded available supplies. Whether silica concentrations in Lake Ontario will increase in the future will likely depend on whether the silica demand in Lake Erie decreases in response to reduced phosphorus loading.

Carbon

Rates of organic carbon accumulation were low under pristine conditions, then increased moderately after forest clear-

ance, and finally increased exponentially during the period of urban loading (Fig. 5). Increases in organic carbon accumulation coincide very well with the results of Chapra's (1977) model of increases in total phosphorus (Fig. 2). Organic carbon is the only nutrient which has a temporal pattern that fits the generally accepted concept of historical eutrophication of the Great Lakes. A similar pattern would be expected for either total nitrogen or organic nitrogen, but few data are currently available. Organic carbon also provides an indication that the trophic state has changed in response to decreased phosphorus loading. Both the accumulation rate and $\delta^{13}C$ of organic carbon provide a signal which has been interpreted as a reflection of decreased primary production during winter–spring mixing since the mid-1970s (Schelske and Hodell 1988).

The paleolimnological record shows that biologically induced carbonate precipitation, which had been observed on lake-wide basis in the 1970s (Strong and Eadie 1978), is a relatively recent epilimnetic phenomenon in Lake Ontario. It did not become important until the 1940s when calcite accumulation in sediments began to increase rapidly during the period of increased urban phosphorus loads (Schelske et al. 1988).

Production of organic carbon and precipitation of calcite would be expected to decrease in the future in response to reduced phosphorus supplies (Fig. 5). Decreases are expected because both processes are dependent on rates of primary production which should decrease in response to lower phosphorus concentrations in this phosphorus-limited lake. A decrease in production of organic carbon in response to lower winter–spring phosphorus concentrations (Fig. 4) appears to be reflected by reduced organic carbon accumulation in the sediments as discussed above. However, precipitation of calcite may decrease less than production of organic carbon if the summer epilimnetic phosphorus concentration continues to decrease less than the winter–spring concentration (see Lean et al. 1987).

Importance of the Paleorecord for Future Research

The field of paleolimnology has expanded rapidly in the past decade and offers many possibilities for future research on aquatic systems (Smol 1990). Paleolimnological techniques can be developed and calibrated to obtain information that is not available from long-term monitoring (Schindler 1987; Smol 1989). In particular, diatom microfossils in the sediments may record an integration of water column processes, particularly seasonality, that may be difficult to resolve with conventional sampling (Hecky and Kilham 1973). Such an integrated record is especially important for the Laurentian Great Lakes because of the logistic problems in sampling such large lakes and because the historical data base is limited. Historically, sampling the Great Lakes has been limited during the period from late autumn to early spring because of adverse weather. Finally, paleolimnological approaches offer potential for describing and then testing hypotheses on natural variability in systems processes.

Data reviewed here indicate that additional paleolimnological studies will provide new insights. Finely sectioned cores collected at high-sedimentation sites can be used to obtain better resolution of historic events and variability. Comparison of data from several cores collected in 1987 (Schelske and Hodell 1988 and unpublished) with the cores collected in 1981 from stations G32 and E30 shows that better and reproducible resolution of calcite and biogenic silica stratigraphy can be obtained with finer sectioning of cores. Thus, with sectioning at 1.0-cm, or possibly finer, intervals, analysis of cores collected in the future may provide additional insights about historical nutrient enrichment and dynamics and also about relatively recent changes in system properties.

Several stratigraphic markers that have been identified from recent paleolimnological research will be important in future studies of the lower Great Lakes. The peak in biogenic silica accumulation has been proposed as a stratigraphic marker for the period of early forest clearance, about 1865 in Lake Ontario (Schelske et al. 1988). It is a biogeochemical signal that can be used as an event marker which like the *Ambrosia* horizon establishes the period of forest clearance in the stratigraphic record. It is likely that other time horizons can be established from the biogenic silica record (Robbins and Schelske 1988; D. J. Conley and C. L. Schelske, unpublished data) and from interannual or short-term variation in calcite accumulation (Schelske and Hodell 1988). Unique event markers in the form of microfossils undoubtedly could be developed. Spines of *Bythotrephes cederstroemi*, a cladoceran that invaded the lower Great Lakes in 1984, provide such a marker in Lake Erie (Keilty 1988) and should also be useful in Lake Ontario. These event markers, and others that will be developed, will be useful in establishing sediment chronologies for historical studies of anthropogenic loadings and chemical and biological processes.

Interannual variability in primary production in lakes has been related to interannual variability in climatic processes (see Goldman et al. 1989). The onset of thermal stratification and its effect on the duration of epilimnetic primary production has been hypothesized to explain variations in calcite accumulation such as those shown in Fig. 2 (Schelske and Hodell 1988). The period when the water column stratifies, which has varied by as much as 2 mo or from early May to early July (Rodgers 1987), could be a major factor in controlling the magnitude of epilimnetic primary production and in turn of calcite precipitation. Several years with relatively long periods of epilimnetic primary productivity should be reflected in the sediment record by greater calcite accumulation. In addition, interannual variability in other climatically controlled factors such as amount of cloud cover, precipitation, water level, and wind velocity and direction could affect the magnitude of diatom and phytoplankton production. Separate mechanisms related to the phenomenon of El Niño/Southern Oscillation were proposed to explain the observed interannual variability in Castle Lake and Lake Tahoe, the two lakes studied by Goldman et al. (1989).

Investigating natural variability on longer time scales is more amenable to paleolimnological techniques in the Great Lakes. A periodicity of approximately 10-11 yr in biogenic silica accumulation in cores from Lake Erie is being investigated currently (Robbins and Schelske 1988). Although the controlling factors are not known at the moment, these peaks are reproducible among cores, suggesting a link to exogenous factors that might affect diatom production. Peterson et al. (1985, 1986) have shown that interannual variability in river flow affects the silica supply for diatom production in San Francisco Bay.

The historical record of variability in diatom and primary production that can be inferred from the sediment record may have important implications for understanding historical fisheries recruitment. As examples, year-class strength has been linked to periodicities in water level and water temperature (Reckahn 1986) and to water temperature and the 11-yr cycle in sunspot activity (Hartmann 1984). Although Reckahn (1986) suggested that long-term fluctuations in the hydrological cycle and other climatic factors interact to affect fish production,

causal mechanisms to explain interannual variations in the biological responses that account for year-class strength have not been investigated. Hypotheses that food availability for larval and young-of-the year fish depends on climatically controlled interannual variations in water column primary production and epilimnetic primary production could be proposed to account for year-class strength. In years with late thermal stratification, the period of winter–spring production would be extended and relatively greater quantities of organic matter would be produced and sedimented for benthic production (Gardner et al. 1985) whereas in years with early thermal stratification, epilimnetic zooplankton production would be favored (Scavia and Fahnenstiel 1987). A strong link between climatic factors and epilimnetic zooplankton production is certainly suggested for Lake Ontario in 1983 when thermal stratification was the earliest for 21 yr that were studied (Rodgers 1987) and zooplankton standing crop was twofold greater than in any year from 1981 to 1985 (Johannsson 1987).

Expected effects of phosphorus abatement measures, instituted in the mid-1970s, on chlorophyll and zooplankton standing crops (Stevens and Neilson 1987; Taylor et al. 1987; Johannsson 1987) and other indicators of trophic state (Lean et al. 1987) have not been found from water column sampling. Two paleolimnological studies of siliceous microfossils, however, indicate that the trophic state of the lake was affected by the early 1980s in response to reduced phosphorus supplies (Stoermer et al. 1985a, 1985b). In addition, the sediment record of organic carbon and stable carbon isotopes provides evidence that phosphorus abatement programs resulted in a decrease in winter–spring phytoplankton production but not in summer epilimnetic primary production (Schelske and Hodell 1988 and unpublished). Summer epilimnetic phytoplankton production may not have decreased because summer epilimnetic phosphorus levels since the mid 1970s have not decreased as much as spring levels (Stevens and Neilson 1987; Lean et al. 1987). Preliminary paleolimnological data thus may explain why the expected decrease in chlorophyll standing crop in response to phosphorus abatement has not been found from water column sampling.

New nutrient paradigms presented in this paper have been based on paleolimnological evidence from a limited number of cores. However, differences in patterns of nutrient accumulation (Schelske et al. 1988) and in inventories of nutrients (Table 1) have been found for two cores from closely spaced stations in the Rochester Basin of Lake Ontario. Additional studies based on a larger number of cores are needed to confirm that these conclusions about nutrients are applicable to entire depositional basins as well as for the lake basin.

Paleolimnological techniques can be used to obtain sediment loss terms for historical studies of mass balances. A large number of cores may be needed to obtain basin-wide inventories of the material of interest because mass sedimentation and other accumulation rates vary over depositional basins as the result of sediment focusing (Schelske et al. 1988). It may be possible, however, to use focusing factors to obtain basin-wide accumulation rates from a limited number of cores (see Eisenreich et al. 1989).

Simulation modelling of total phosphorus in the Great Lakes by Chapra (1977) has provided important insights about historical total phosphorus loading and in-lake total phosphorus concentrations and sediment losses. Sediment loss is the only term in historical mass balances that can be verified by measurement. The sediment record can be used to verify loss terms, basin-by-basin, for these mass balances. Given the importance of phosphorus control in the management of the Great Lakes, it is somewhat surprising that losses of this nutrient have not been obtained directly using paleolimnological techniques. One of the important areas for future paleolimnological study will be to obtain estimates of sediment loss for historical mass balances of nutrients. The data generated would be valuable in validating assumptions that have been used in modelling of phosphorus, in developing new models of major nutrients, and in understanding nutrient dynamics and processing.

Acknowledgments

I would like to thank R. W. Flint for his invitation and encouragement to initiate this work and R. W. Howarth and two anonymous reviewers for providing helpful criticism on the manuscript. This work was supported by National Science Foundation grant OCE-8722983 to Claire L. Schelske.

References

BEETON, A. M. 1965. Eutrophication of the St. Lawrence Great Lakes. Limnol. Oceanogr. 10: 240–254.

1969. Changes in the environment and biota of the Great Lakes, p. 150–187. *In* Eutrophication: causes, consequences, correctives. National Academy of Sciences, Washington, D.C.

BILBY, R. 1981. Role of organic debris dams in regulating the export of dissolved and particulate matter from a forested watershed. Ecology 62: 1234–1243.

CHAPRA, S. C. 1977. Total phosphorus model for the Great Lakes. J. Environ. Eng. Div. 103: 147–161.

DOBSON, F. H. 1984. Lake Ontario water chemistry atlas. Natl. Water Res. Inst., Canada Centre Inland Waters, Burlington, Ont., Sci. Ser. No. 139: 59 p.

EISENREICH, S. J., P. D. CAPEL, J. A. ROBBINS, AND R. BOURBONNIERE. 1989. Accumulation and diagenesis of chlorinated hydrocarbons in lacustrine sediments. Environ. Sci. Technol. 23: 1116–1126.

GARDNER, W. S., T. F. NALEPA, W. A. FREZ, E. A. CICHOCHI, AND P. F. LANDRUM. 1985. Seasonal pattern in lipid content of Lake Michigan macroinvertebrates. Can. J. Fish. Aquat. Sci. 42: 1827–1832.

GOLDMAN, C. R., A. JASSBY, AND T. POWELL. 1989. Interannual fluctuations in primary production: meteorological forcing at two subalpine lakes. Limnol. Oceanogr. 34: 310–323.

HARRIS, G. P., AND R. A. VOLLENWEIDER. 1982. Paleolimnological evidence of early eutrophication in Lake Erie. Can. J. Fish. Aquat. Sci. 39: 618–626.

HARTMANN, J. 1984. 11-year cycle of spawning time and growth of the whitefish (*Coregonus lavaretus*) of Lake Constance. Schweiz. Z. Hydrol. 46: 163–170.

HECKY, R. E., AND P. KILHAM. 1973. Diatoms in alkaline, saline lakes: ecology and geochemical implications. Limnol. Oceanogr. 18: 53–71.

HEDIN, L. O., M. S. MAYER, AND G. E. LIKENS. 1988. The effect of deforestation on organic debris dams. Verh. Int. Ver. Limnol. 23: 1135–1141.

INTERNATIONAL JOINT COMMISSION. 1988. Rehabilitation of Lake Ontario: the role of nutrient reduction and food web dynamics. Report to the Great Lakes Science Advisory Board. 75 p.

JOHANNSSON, O. 1987. Comparison of Lake Ontario zooplankton communities between 1967 and 1985: before and after implementation of salmonid stocking and phosphorus control. J. Great Lakes Res. 13: 328–339.

KEILTY, T. J. 1988. A new biological marker layer in the sediments of the Great Lakes: *Bythotrephes cederstroemi* (Schödler) spines. J. Great Lakes Res. 14: 369–371.

KELTS, K., AND K. J. HSU. 1978. Freshwater carbonate sedimentation, p. 295–323. *In* A. Lerman [ed.] Lakes chemistry geology physics. Spring-Verlag, New York, NY.

KEMP, A. L. W., C. B. J. GRAY, AND A. MUDROCHOVA. 1972. Changes in C, N, P, and S in the last 140 years in three cores from Lakes Ontario, Erie, and Huron, p. 251–279. *In* H. E. Allen and J. R. Kramer [ed.] Nutrients in natural waters. Wiley Interscience, New York, NY.

KEMP, A. L. W., AND N. S. HARPER. 1976. Sedimentation rates and a sediment budget for Lake Ontario. J. Great Lakes Res. 2: 324–340.

LEAN, D. R. S., H. J. FRICKER, M. N. CHARLTON, R. L. CUHEL, AND F. R. PICK. 1987. The Lake Ontario life support system. Can. J. Fish. Aquat. Sci. 44: 2230–2240.

NEILSON, M. A., AND R. J. J. STEVENS. 1987. Spatial heterogeneity of nutrients and organic matter in Lake Ontario. Can. J. Fish. Aquat. Sci. 44: 2192–2203.

PETERSON, D. H., D. R. CAYAN, AND J. F. FESTA. 1986. Interannual variability in biogeochemistry of partially mixed estuaries: dissolved silica cycles in northern San Francisco Bay, p. 123–138. *In* Estuarine variability. Academic Press, Inc., New York, NY.

PETERSON, D. H., R. E. SMITH, S. W. HARGER, D. D. HARMON, R. E. HERNDON, AND L. E. SCHEMEL. 1985. Interannual variability in dissolved inorganic nutrients in northern San Francisco Bay estuary. Hydrobiologia 129: 37–58.

RAIDT, H., AND R. KOSCHEL. 1988. Morphology of calcite crystals in hardwater lakes. Limnologica 19: 3–12.

RECKAHN, J. A. 1986. Long-term cyclical trends in growth of lake whitefish in South Bay, Lake Huron. Trans. Am. Fish. Soc. 115: 787–804.

ROBBINS, J. A., AND C. L. SCHELSKE. 1988. Biogenic silica deposition in Lake Erie since 1800. EOS 69: 1143. (Abstract)

RODGERS, G. K. 1987. Time of onset of full stratification in Lake Ontario in relation to lake temperatures in winter. Can. J. Fish. Aquat. Sci. 44: 2225–2229.

SCAVIA, D., AND G. L. FAHNENSTIEL. 1987. Dynamics of Lake Michigan phytoplankton: mechanisms controlling epilimnetic communities. J. Great Lakes Res. 13: 103–120.

SCHELSKE, C. L. 1988. Historic trends in Lake Michigan silica concentrations. Int. Rev. Gesamten Hydrobiol. 73: 559–591.

SCHELSKE, C. L., D. J. CONLEY, E. F. STOERMER, T. L. NEWBERRY, AND C. D. CAMPBELL. 1986a. Biogenic silica and phosphorus accumulation in sediments as indices of eutrophication in the Laurentian Great Lakes. Hydrobiologia 143: 79–86.

SCHELSKE, C. L., D. J. CONLEY, AND W. F. WARWICK. 1985. Historical relationships betwen phosphorus loading and biogenic silica accumulation in Bay of Quinte sediments. Can. J. Fish. Aquat. Sci. 42: 1401–1409.

SCHELSKE, C. L., AND D. A. HODELL. 1988. Historic and interannual productivity changes in Lake Ontario from isotopic analysis of sediments. EOS 69: 1083. (Abstract)

SCHELSKE, C. L., J. A. ROBBINS, W. D. GARDNER, D. J. CONLEY, AND R. A. BOURBONNIERE. 1988. Sediment record of biogeochemical responses to anthropogenic perturbations of nutrient cycles in Lake Ontario. Can. J. Fish. Aquat. Sci. 45: 1291–1303.

SCHELSKE, C. L., E. F. STOERMER, D. J. CONLEY, J. A. ROBBINS, AND R. M. GLOVER. 1983. Early eutrophication in the lower Great Lakes: new evidence from biogenic silica in sediments. Science (Wash., DC) 222: 320–322.

SCHELSKE, C. L., E. F. STOERMER, G. L. FAHNENSTIEL, AND M. HAIBACH. 1986b. Phosphorus enrichment, silica utilization, and biogeochemical silica depletion in the Great Lakes. Can. J. Fish. Aquat. Sci. 43: 407–415.

SCHINDLER, D. W. 1987. Detecting ecosystem responses to anthropogenic stress. Can. J. Fish. Aquat. Sci. 44 (Suppl. 1): 6–25.

SMOL, J. P. 1989. Paleolimnology — recent advances and future challenges. *In* R. De Bernardi, G. Guissani, and L. Barbanti [ed.] Scientific perspectives in theoretical and applied limnology. Mem. Ist. Ital. Idrobiol. 47: 247–272.

STEVENS, R. J. J., AND M. A. NEILSON. 1987. Response of Lake Ontario to reductions in phosphorus load, 1967–82. Can. J. Fish. Aquat. Sci. 44: 2059–2068.

STOERMER, E. F., G. EMMERT, AND C. SCHELSKE. 1989. Morphological variation of *Stephanodiscus niagarae* Ehrenb. (Bacillariophyta) in a Lake Ontario sediment core. J. Paleolimnol. 2: 227–236.

STOERMER, E. F., J. P. KACIOLEK, C. L. SCHELSKE, AND D. J. CONLEY. 1987. Quantitative analysis of siliceous microfossils in the sediments of Lake Erie's central basin. Diatom Res. 2: 113–134.

STOERMER, E. F., J. A. WOLIN, C. L. SCHELSKE, AND D. J. CONLEY. 1985a. An assessment of ecological changes during the recent history of Lake Ontario based on siliceous algal microfossils preserved in the sediments. J. Phycol. 21: 257–276.

1985b. Variations in *Melosira islandica* valve morphology in Lake Ontario sediments related to eutrophication and silica depletion. Limnol. Oceanogr. 30: 414–418.

1985c. Postsettlement diatom succession in the Bay of Quinte, Lake Ontario. Can. J. Fish. Aquat. Sci. 42: 754–767.

STRONG, A. E., AND B. J. EADIE. 1978. Satellite observations of calcium carbonate precipitations in the Great Lakes. Limnol. Oceanogr. 23: 877–887.

TAYLOR, W. D., H. J. FRICKER, AND D. R. S. LEAN. 1987. Zooplankton seasonal succession in Lake Ontario at northshore, midlake, and southshore stations in 1982, and a comparison with 1970. Can. J. Fish. Aquat. Sci. 44: 2178–2184.

THOMAS, R. L., A. L. W. KEMP, AND C. F. M. LEWIS. 1972 . Distribution, composition and characteristics of the surficial sediments of Lake Ontario. J. Sediment. Petrol. 42: 66–84.

WARWICK, W. F. 1980. Paleolimnology of the Bay of Quinte, Lake Ontario: 2,800 years of cultural influence. Can. Bull. Fish. Aquat. Sci. 206: 117 p.

Submerged Macrophytes in Lake Ontario: Current Knowledge, Importance, Threats to Stability, and Needed Studies

A. Crowder

Department of Biology, Queen's University, Kingston, Ont. K7L 3N6, Canada

and D. S. Painter

Environment Canada, Lakes Research Branch, Canada Centre for Inland Waters, P.O. Box 5050, Burlington, Ont. L7R 4A6, Canada

Crowder, A., and D. S. Painter. 1991. Submerged macrophytes in Lake Ontario: current knowledge, importance, threats to stability, and needed studies. Can. J. Fish. Aquat. Sci. 48: 1539–1545.

The submerged limnetic community in Lake Ontario includes algae, bryophytes, and about 30 species of angiosperms. Their distribution is accurately known in some areas but not lake-wide, and a whole-lake survey is recommended. In nutrient cycling, submergents act as sinks during the summer; metals and metalloids occur in high concentrations in tissues from some areas. Known herbivores include invertebrates, fish, and waterfowl. Stands are necessary for many fish taxa as breeding or nursery habitats, and for waterfowl, but may be damaged by carp (*Cyprinus carpio*). Stability has been affected by water levels, sedimentation, wave and ice movement, invasive species, herbivory, eutrophication and turbidity, and contaminants. Recovery after control of P loading has occurred in Irondequoit Bay but is delayed by turbidity in the Bay of Quinte.

La communauté limnétique submergée du lac Ontario comprend des algues, des bryophytes et environ trente espèces d'angiospermes. Étant donné que leur répartition précise n'est connue qu'à quelques endroits du lac, on recommande qu'un relevé global soit réalisé. Dans le cycle des éléments nutritifs les végétaux submergés agissent comme piège pendant l'été; les métaux et les métalloïdes sont retrouvés en grandes concentrations dans les tissus de plantes échantillonnés à certains endroits. Les herbivores connus comprennent des invertébrés, des poissons et des oiseaux aquatiques. Les peuplements de végétaux servent à de nombreuses espèces de poissons comme frayère ou zone d'alevinage, et à de nombreuses espèces d'oiseaux aquatiques, mais ils peuvent être endommagés par la carpe (*Cyprinus carpio*). La stabilité des communautés végétales a été touchée par les niveaux de l'eau, la sédimentation, les vagues et les glaces, les espèces envahissantes, l'eutrophisation, la turbidité, les herbivores et les éléments polluants. On a noté le rétablissement de la communauté végétale dans la baie Irondequoit après que la charge de P ait été réduite, mais il est retardé par la turbidité dans la baie de Quinte.

Received January 24, 1989
Accepted October 22, 1990
(JA034)

Reçu le 24 janvier 1989
Accepté le 22 octobre 1990

When a functional model of the ecosystem of Lake Ontario is constructed, submergent macrophytes must be considered as a compartment for energy fixation and nutrient flux. Is this compartment negligible, or does it have a significant role, for example as fish habitat or in providing food for migrant waterfowl? This paper seeks to evaluate our present knowledge of the submergent macrophytes in the lake and to point out where research is necessary. The questions asked are: What is the composition of the community, what is the distribution of the community, what is the role of submergent vegetation in nutrient cycling and food webs, what is its function as habitat, and what are the threats to its stability?

What is the Composition of the Submergent Community?

There has been no lake-wide survey of submergent vegetation except for the macroalga *Cladophora* (Painter and Kamaitis 1985). A taxonomic list can be compiled from the numerous small-scale surveys which have been made, and relative specific abundance, cover, and biomass are known for some areas such as the Bay of Quinte.

The flowering plants found as submergents (some of which can also occur as emergents) in the northeast end of the lake include *Najas flexilis*, *N. guadalupensis*, *Potamogeton crispus*, *P. friesii*, *P. nodosus*, *P. pectinatus*, *P. pusillus*, *P. perfoliatus* (spp. *richardsonii*), *P. zosterifolius* (spp. *zosteriformis*), *Zannichellia palustris*, *Alisma gramineum*, *Sagittaria latifolia*, *Elodea canadensis*, *Vallisneria americana*, *Hydrocharis morsus-ranae*, *Eleocharis acicularis*, *Lemna trisulca*, *Heteranthera dubia*, *Polygonum amphibium*, *Ceratophyllum demersum*, *Nuphar variegatum*, *Nymphaea odorata*, *N. tuberosa*, *Ranunculus aquatilis*, *R. trichophyllus*, *Myriophyllum spicatum*, *M. exalbescens*, *Utricularia intermedia*, and *U. minor* (Crowder et al. 1977; Crowder and Bristow 1986; Ruta 1981). Identifications have been confirmed by experts and voucher specimens preserved (Crowder et al. 1977; Crowder and Bristow 1986); the nomenclature used in this paper is that used in these references and has not been brought up to date. *Najas guadalupensis* is listed as rare in Ontario (Argus and White 1977) but is locally abundant in the Bay of Quinte.

In the area from Clayton to the Black River, Geis and Kee (1977) reported a similar list with the addition of *Potamogeton foliosus* and *Myriophyllum heterophyllum*. On the south side of the lake, at Irondequoit Bay, additions to this list reported until

1939 included *Najas marina*, *Potamogeton pulcher*, and *Sparganium minimum* (Bannister and Bubeck 1978). *Myriophyllum spicatum*, *Potamogeton crispus*, and *Hydrocharis morsus-ranae* are invasive species of European origin: *P. crispus* arrived earliest, *M. spicatum* probably reached Lake Ontario by the 1950s and *H. morsus-ranae* by the 1970s (Crowder and Bristow 1986). *Hydrocharis morsus-ranae* is generally found floating in waterlily or cattail beds but has been found growing submerged in the lower Bay of Quinte (A. Crowder, unpubl. data). Nonflowering plants include bryophytes, of which the most abundant are *Drepanocladus* spp. (Crowder and Bristow 1986). Macroalgae include Characeae, green filamentous taxa, and an attached red alga. *Chara braunii*, *C. globularis*, *C. vulgaris*, and *Nitella flexilis* are common in the Quinte area (Crowder and Bristow 1986); close to the St. Lawrence River, *Nitellopsis obtusa*, a species introduced from South America, is now abundant (Ruta 1981); it was first reported there in 1978 and has since been found elsewhere in the Great Lakes (Schloesser et al. 1986). The attached green algae are mostly *Spirogyra* and *Cladophora* spp. *Cladophora* became a nuisance during the 1960s and was therefore sampled several times in the subsequent decades: it dominates rocky parts of the shore (Painter and Kamaitis 1985). The red alga *Bangia atropurpurea* was first reported in the lake in 1966 (Sheath and Cole 1980; Hamilton and Wilson-Neish 1988). It grows at or below the waterline, above *Cladophora*, and tolerates a wide range of salinity. It is thought to have been introduced on the hulls of ocean-going ships.

There is a need for a floristic survey using a consistent method all around the lake; it should relate submerged vegetation to the vegetational gradients upslope. Most wetland surveys arbitrarily stop sampling at a depth of 2 m, thus truncating information on the lower parts of the shore, but a whole-lake survey should extend to the lower limit of submerged growth to investigate changes in diversity and biomass. A survey should also measure physical and chemical properties of the water and substrate, and the geographical properties of shores such as fetch, so that the submergent vegetation can be classified and ordinated. It is obvious, for example, that floating-leaved vegetation occurs in sheltered sites, but few data exist from Lake Ontario to substantiate this statement.

What is the Distribution of the Submergent Vegetation?

Apart from maps of *Cladophora*, there is no uniform mapping of submerged vegetation. Twenty coastal marshes on the north shore have been listed as provincially or regionally significant by Glooschenko et al. (1987), but the methods of evaluation do not provide maps of submerged zones. The offshore beds at Wolfe and Amherst islands have been described by Bottomley (1986) because of their importance to migant waterfowl. Sites where detailed surveys have been made on the north shore include Coote's Paradise, Rouge River, Oshawa Second Marsh, Rattray Marsh, Presqu'ile Provincial Park, Bay of Quinte to Gananoque, Big Island Marsh, Gravelly Big Marsh, Nut Island Club Marsh, and Great Cataraqui Marsh (for references, see Crowder and Bristow 1988). In addition, unpublished surveys have been made by the Ontario Ministry of Natural Resources, by conservation authorities, by the Canadian Wildlife Service, and by the Parks Service of Environment Canada. Several unpublished records exist for the New York shore. Published surveys in the St. Lawrence River area include those of Geis and Kee (1977) and Ruta (1981) and in Irondequoit Bay that of Forest (1987).

There is thus a wealth of distributional information, but it has been collected at different times and using different protocols so that our integrative knowledge of the submerged macrophyte community is limited. To provide documentation of current status of the limnetic zone and a basis for investigating changes, a lake-wide survey is needed, possibly using remote sensing data transferred to a geographic information system. The efficiency of LANDSAT thematic mapping verified by divers has been discussed by Bottomley et al. (1987).

What is the Role of the Submergents in Nutrient and Element Cycling?

Although the productivity of the submergents has not been measured, biomass for some areas has been estimated, as has P content in the Bay of Quinte (Crowder and Bristow 1986). Biomass of *Cladophora* was estimated by Painter and Kamaitis (1985); it fell from a mean of 106 $g \cdot m^{-2}$ in 1972 to 86 $g \cdot m^{-2}$ in 1983, as point source P inputs to Lake Ontario decreased. Submergent biomass from all vegetated depths in the Bay of Quinte averaged only 25 $g \cdot m^{-2}$ in 1972–82 (Crowder and Bristow 1986) but rose to 36 $g \cdot m^{-2}$ by 1988 (A. Crowder, unpubl. data). Variance was high and samples were heavier in the shallows (Limnos Ltd. 1989). In the less turbid waters at the outflow to the St. Lawrence River, biomass above depths of 3 m averaged 307 $g \cdot m^{-2}$ (Ruta 1981). In these sampling sites the usual decrease of biomass with increasing depth was found, with a mean value of 191 $g \cdot m^{-2}$ below 3 m.

Elements cycle seasonally through the submergents because most of the biomass builds up and decays annually, leaving roots, bases, apices, or seeds to overwinter. The overwintering parts may remain in situ or move (Crowder and Bristow 1986). Nutrients are thus added to water or sediment in the fall and winter. Great Lakes marshes are not efficient nutrient sinks even in the emergent zones (Spencer et al. 1984). Wetzel, working at Lawrence Lake in Michigan, has quantified passage of nutrients between submergents, sediments, aufwuchs (the microflora growing on submergents), and water. He found that nutrients pumped from sediment into plants can (a) be leaked into the lake water, (b) pass into aufwuchs with very little loss to the water, and (c) pass into microflora on the death of the plants, again with little loss to the lake water. The loading of nutrients to the lake varied, for example nitrate-N movement to the water was diminished by the plant–aufwuchs combination, but loading of dissolved organic N compounds into the water was increased (Wetzel 1990). Without similar research in Lake Ontario, it is not possible to assess the magnitude of nutrient cycling in the submergent area.

Organic C and P in sediments were positively correlated with plant cover at 42 sites with a depth of 0.5 m in the Bay of Quinte (Dushenko et al. 1989). The correlation suggests that C and P are added to the substrate by the plants; an alternative hypothesis, that the plants select sites with higher C and P, was rejected on the basis of transplant experiments (Dushenko et al. 1990).

There is potential contamination of submergents by metals and metalloids in Lake Ontario marshes because elevated concentrations of As, Cd, Cr, Fe, Hg, Mn, Ni, Zn, and other metals have been measured at several sites. These include Oshawa Second Marsh, Rattray Marsh, Coote's Paradise, and the Bay of Quinte (Glooschenko 1978; Mudroch 1981; McLarty and

Thachuk 1986; Weseloh et al. 1987). Mudroch et al. (1988) have collated data on metal distribution and concentration from Great Lakes sites.

Uptake was found, as is usually the case to be species specific in the Bay of Quinte. Pb, for example, was 6–6.5 $\mu g \cdot g^{-1}$ in *Myriophyllum spicatum* and less than 1.1 $\mu g \cdot g^{-1}$ in *Vallisneria americana* collected at the same eight sites. The concentration pattern was reversed for Na (*V. americana*, 2.3–2.4%, *M. spicatum*, (0.6%). Significant differences also occurred within species between sites (Crowder et al. 1989).

Sediment and plant values for Al, Mg, and V were positively correlated in the Bay of Quinte, using *Hydrocharis morsus-ranae* as a test plant (*H. morsus-ranae* is usually a floating plant, but also occurs as a submergent). Ranges of element concentrations in *H. morsus-ranae* ($n = 60$) were as follows: Al, 129–1450 ppm; As, 0–63 ppm; Ca, 0.3–3.1%; Cl, 0.65–1.54%; Cu, 2–266 ppm; Ni, 0–262 ppm; V, 0.6–15.5 ppm (Greig 1989; Greig et al. 1989). These values show potentially toxic concentrations of some metals such as Ni and Cu, but in snails feeding on the *Hydrocharis* the only element positively correlated with amounts in the plants was Ca. This lack of transfer to herbivores may not be typical, since positive correlations of plant metals and metals in herbivores are known from wetlands elsewhere, for example Cd and Pb in roots of cattail (*Typha angustifolia*) and in tissues of muskrats (*Ondatra zibethicus*) (Everett and Anthony 1976; Erichson and Lindzey 1983).

What is the Role of Submergents as Food?

Several types of herbivores eat submergents, including nematodes (Smart *et al.* 1987) and relatively large invertebrates. Declines of *Myriophyllum spicatum* are attributed to feeding by insects, including the larvae of *Acentria nivea* in the Kawartha Lakes immediately north of Lake Ontario (Painter and McCabe 1988) and dipteran larvae in the Thousand Islands region (Oliver 1984).

Larger herbivores include carp (*Cyprinus carpio*). Stomach analyses of carp from the Bay of Quinte contain submergents (Powles et al. 1983). Carp are extremely numerous in shallow areas such as Coote's Paradise, the Bay of Quinte, and Great Cataraqui Marsh. Fresh plant material also forms about 13% of the diet of snapping turtles (*Chelydra serpentina*) and 10% of that of bluegills (*Lepomis macrochirus*) (Townsend 1979; Moll 1985; Engel 1987), but no data from Lake Ontario are available for these taxa or for crayfish. The most important trophic interaction may be the flow of nutrients into waterfowl. Submergent stands are used by both migratory and nesting birds (Carter and Haramis 1980; Curtis et al. 1984), most intensely in the Burlington–Toronto and Prince Edward County areas. The binational importance of the Great Lakes marshes as habitat for waterfowl was emphasized in the North American Waterfowl Management Plan (Environment Canada et al. 1986), as there is general alarm about declines in the continental waterfowl populations. Plants found in stomach analyses of 15 species of waterfowl and their distribution in nine Lake Ontario coastal wetlands were tabulated by Crowder and Bristow (1988). No calculation of the biomass eaten annually throughout the lake has been made.

The submerged zone is not generally regarded as a prime habitat for muskrats, but elsewhere they graze on submerged swards, for example on *Eleocharis* (Fuller et al. 1984).

What is the Role of Submergents as Habitat?

Submergents add structure to the shoreline, creating habitat for invertebrates and young and small fish. Johnson and Brinkhurst (1971) found a distinct littoral assemblage of invertebrates associated with vascular plants, including chironomids, isopods, amphipods, mayflies, and lepidopterans in the Bay of Quinte. Associations of invertebrates with submergents are specific (Gerrish and Bristow 1979); for example, species of invertebrates associated with the invasive *Myriophyllum spicatum* differ from the invertebates associated with neighbouring native plants (Keast 1984). Mixed plant communities contained more fish in the Rideau lakes, a tributary system of Lake Ontario, than did monospecific stands of milfoil.

Fish which lay eggs in submergent stands include northern pike (*Esox lucius*), perch (*Perca flavescens*), and largemouth bass (*Micropterus salmoides*). In five coastal marshes near Toronto, Stephenson (1989) has found over 20 fish species using the wetland during the breeding season. These include pumpkin seed (*Lepomis gibbosus*), carp, and stone roller (*Hypentelium nigricans*). Young-of-the-year made maximal use of the nursery habitat from May to July. Associations of fish with plants are being investigated at Hamilton Harbour and the Bay of Quinte, as part of Remedial Action Programmes (V. Cairns, N.W.R.I., P.O. Box 5050, Burlington, Ont. L7R 4A6, pers. comm.).

Total yields of fish are positively correlated with the area of submergent vegetation in the tributary Trent–Rideau system (Whillans 1989), and closer correlations are found for warmwater fish. In general, fish production is lowered if submerged vegetation is removed (Crowder and Cooper 1979; Engel 1987). It has been suggested that declines of lake herring (*Coregonus artedii*) may have been accelerated by loss of beds of *Chara*, over which they spawned (Edsall et al. 1988).

Carp use the submergents and the edges of cattail marshes for both breeding and foraging. Their activities alter the habitat by uprooting plants and disturbing sediments (Painter et al. 1988). In Florida, another species of carp (*Ctenopharynogon idella*) removed all submergents and decreased the Secchi disc depth of a lake from 6 to 1.5 m (Anonymous 1987; Leslie et al. 1987), and in Chesapeake Bay it has been possible to revegetate coastal areas only if carp and turtles are excluded (Carter and Rybicki 1985).

The submergent areas are also part of breeding habitat for ducks and muskrats, the latter often building houses offshore. The submergent zone overall is extremely important as habitat for many groups of animals.

How Stable is the Submerged Plant Community?

Stability and Water Level

The water level of Lake Ontario cycles over a period of 15–20 yr, cycles annually, and also changes over short periods because of seiches and wind (Busch et al. 1989). Such short-term fluctuations have ranged from -0.5 to $+1.75$ m (Fisheries and Environment Canada and Ontario Ministry of Natural Resources 1979). In some marshes, frequent rapid changes have been observed, for example in the lower Napanee River.

Research on the effects of changing levels on vegetation has concentrated on the upper parts of marshes (Cecile 1983; Kelley et al. 1985; Patterson and Whillans 1985; Quinlan and

Mulamootil 1987). Presumably the submergents can move up and down the shore as levels change, provided slopes are even and the changes of level are not too rapid; thus, the changes in area of open water (14–48% of total marsh area) reported by Quinlan and Mulamootil (1987) in wetlands near Toronto and Oshawa presumably represent changes in potential submergent habitat.

A phase of extremely low water exposed submergents in the Bay of Quinte from March to May in 1988 and 1989; this exposure appeared to have little effect on submergents, as biomass returned to normal by July each year (A. Crowder, unpubl. data). These periods of low water increased the area of the emergent wild rice (*Zizania aquatica*) on mud flats; Keough (1986) found that low water favoured its germination.

Long-term monitoring of selected transects perpendicular to the shore is necessary to investigate local effects of changing water levels on submerged plants. This has been started at some sites (e.g. in the Bay of Quinte; A. Crowder, unpubl. data).

Stability and Temperature

Local warming due to power stations has been reported (Stephenson 1989), but not its effects on submergents. Predicted effects would be an increase in biomass and species richness, as plants at present confined to Lake Erie could move north. In Lake Erie, local warming keeps some areas open in winter, resulting in increased numbers of overwintering ducks.

Stability, Water and Ice Movement, and Sedimentation

Plant cover at 42 sites in the Bay of Quinte was directly related to fetch, slope, and the particle size of sediment (Dushenko et al. 1989). As expected, extremely exposed shores are devoid of submergents because of wave action and the formation of storm beaches, for example on the Duck Islands. The filamentous algae are the group best adapted to such exposed conditions. Submergents can be destroyed by a single storm; no records were found from Lake Ontario, but in the Finger Lakes in New York State a hurricane decreased biomass and diversity through increased turbidity (Oglesby 1978). Death of *Vallisneria americana* from burial in silt has been reported after a single storm in the Chesapeake Bay region (Rybicki and Carter 1986).

Disruption of submerged vegetation by ice was described in the upper St. Lawrence marshes by Geis (1985). An icefoot incorporating sediments extended into the wetland and was deeper and larger in years with low water levels in early winter. In spring, melting began in stream channels and moved outward from the shore, while the outer ice stayed solid. Floes were detached, and sediment and vegetation moved. Geis measured grounded ice 40–50 m offshore in bays and 5–10 m off rocky shores, resulting in low biomass and species richness in these areas during the next summer. Crowder and Bristow (1986) found low species richness close to shore, possibly because of ice action. The thickness and movement of ice varied greatly from year to year, thus affecting the stability of the vegetation.

Effects of Invasive Species

Effects of the invasive algae *Nitellopsis* and *Bangia* are not known. The most notable flowering invader is *Myriophyllum spicatum*, eurasian milfoil. It had been introduced by the 1950s and was dominant in some areas by the 1960s. In the Bay of Quinte it was the species creating most cover from 1972 to 1986, since when it has been surpassed by *Vallisneria americana* and *Heteranthera dubia* (A. Crowder, unpubl. data). Milfoil's competitive success may be attributed to its ability to grow very early in the year, to form a canopy, and to thrive in a turbid milieu high in nutrients and salt; in field replacement experiments, Les et al. (1988) found that site factors were more important than direct competition in determining the relative success of milfoil and species of *Potamogeton*. Its current decline may be due to herbivory by insects (Oliver 1984; Painter and McCabe 1988). *Hydrocharis morsus-ranae*, frogbit, is another rapidly spreading invader, mostly in cattail and floating-leaved stands, but also in submerged areas.

Contemporaneously with increases in milfoil, native species have been lost. In Irondequoit Bay, for example, *Potamogeton pulcher*, *Najas marina*, and *Sparganium minimum* were not found after 1939 (Bannister and Bubeck 1978). Generally, the number of species of *Potamogeton* has declined.

Effects of Herbivory on Stability

Herbivory by insects on milfoil has already been mentioned, as has the less specialized feeding of carp. An indication of the importance of carp is given by the quantity caught during 1952–56, some 93 000 fish in Coote's Paradise, an area of 250 ha. Carp not only eat submergents, but stir up sediment and increase turbidity (Painter et al. 1988), preventing reestablishment of plants.

Herbivory by migratory birds has probably become more concentrated because of decreases in the area of submerged vegetation such as those observed around Lake Ontario (Forest 1987; Crowder and Bristow 1986). This concentration of ducks has been recorded in the Mississippi River, where large numbers congregate on the remaining stands of *Vallisneria americana* (Korschgen et al. 1988).

Effects of Eutrophication on Stability

The depth to which plants grow is determined by light quantity and quality (Duarte and Kalff 1988; Chambers and Kalff 1987; Chambers and Prepas 1988). Eutrophication allows phytoplankton to increase, shading the macrophytes beneath. In open areas of Lake Ontario the bottom limit for submergents ranges down to 9 m (Crowder and Bristow 1986). In the hypereutrophic conditions of the Bay of Quinte, however, the macrophytes could only grow down to 2 m during the period 1972–82 (Crowder and Bristow 1986). In the prevailing turbidity (with a mean Secchi disc reading of 1.07 m), biomass and species richness were also low. Temporal decrease in diversity has been well documented at Coote's Paradise, with a species richness of 24 in the 1940s, falling to 11 in 1968–72 and 4–5 in the 1980s as eutrophication and turbidity increased.

Turbidity is not due solely to algae. In Coote's Paradise, current Secchi disc depths do not correlate with chlorophyll measurements, although algal biomass is high. They are correlated with seston, mostly mineral in origin. The numerous carp cause resuspension of silt, the marsh receives effluent from a sewage treatment plant, and run-off in the area is high. Other sites on Lake Ontario have followed the classic model of eutrophication (an early peak of filamentous algae, a rise in submergent biomass, increasing phytoplankton biomass and turbidity, followed by a drastic loss of submergents) including Rattray Marsh and Irondequoit Bay.

Recovery from eutrophication after control of point source inputs of P has been described at Irondequoit Bay (Forest 1987).

Because the bay is almost enclosed, it was possible to augment the control of P inputs with alum treatment of sediments. The result was an increase in light penetration which has allowed a recovery of species richness and an increased area of vegetation. In the Bay of Quinte, control of point source P has not resulted in increased light penetration in the shallows, although phytoplankton biomass in open water has decreased (Minns et al. 1986; Dushenko 1990). The relative effects of seston and plankton on light extinction vary seasonally in this "estuarine" system.

Effects of Contaminants

Contamination of sediment by metals has been documented, for example, in Oshawa Second Marsh, Rattray Marsh, Coote's Paradise, and the Bay of Quinte (Glooschenko 1978; Mudroch 1981; McLarty and Thachuk 1986; Crowder et al. 1989; Dushenko 1990). Metals found in high concentrations include Al, Ag, Cd, Cu, Fe, Hg, Mn, Ni, Pb, and Zn. Plants do not necessarily bioaccumulate or biomagnify these metals from the sediment; site-specific and species-specific differences in metal uptake have been found.

The effect of sodium chloride may be as impotant as that of highy toxic metals, as it has been generally increasing (Beeton 1965) and is augmented by sewage treatment plant effluents and by road salt. The invasion of salt-tolerant *Bangia* has been noted above, and halophilic terrestrial vegetation has been reported near a snow dump in Toronto (Catling and McKay 1975). Elsewhere the effect of salt has been to diminish diversity, for example in Lake Champlain (Schwartz and Gruending 1986) and Cheaspeake Bay (Bayley et al. 1978). Occasional pulses of salt are sufficient to reduce diversity in salt marshes (Valentine 1978) and such pulses occur during spring melting round Lake Ontario; sodium chloride at concentrations measured in waters near Kingston caused specific decreases in biomass and survivorship in experimental cultures (A. Crowder and A. McLaughlin, unpubl. data). Cl^- has been blamed for die-off of submergents at the outfall of power stations, but greater depression of growth was caused by Na^+ in these experiments.

Organic contaminants are mostly herbicides and pesticides. Triazine herbicides, especially atrazine, have been found in significant concentrations in rivers in southern Ontario draining areas of intensive crop production, especially of corn (Crowder and Bristow 1988). The area most likely to be affected in Lake Ontario is the Niagara–Hamilton shore.

Industrial effluents containing organic pollutants are not generally harmful to submergents but have caused some die-offs (Dickman et al. 1983). Leaks and die-offs occur suddenly and ae not often detected; it is therefore not possible to assess their importance in Lake Ontario with current information.

Effects of Acidity

It is generally assumed that Lake Ontario is so well buffered by calcium carbonate that acid precipitation is not a problem and that, because most acidic episodes occur in spring run-off, the submergents are not likely to be affected (Ashworth 1986). The plants tend to lower the pH in their rhizosphere, presumably by addition of organic matter and by unbalanced uptake of ions. During 1988 and 1989, surface water pHs of 7.5–10.1 were measured at shore sites in the Bay of Quinte, at which the pH in the sediment was 5.5–9.3, with a mean of 7.5; in the peaty emergent zone the range was 5.0–7.7 (Dushenko 1990).

Anthropogenic Effects on Stability

The factors discussed above are largely caused indirectly by an increasing human population, controlled water levels, changes in temperatures, introduced new species, etc. Direct human effects include alteration of shorelines by dredging, filling, and construction. Recreational use often results in destruction of vegetation by cutting or use of herbicides. Turbidity is increased by run-off from nonvegetated areas, particularly when new developments are being built. Structures to minimize run-off, such as catchment basins, can be used, as can conservationist techniques of road bulding, etc., but are not mandatory around Lake Ontario. There is no coordinated planning by municipalities around the lake, so that permits for altering the shoreline vegetation are granted without an overall judgement on the contribution of a particular area to the ecology of the whole lake.

Acknowledgments

We wish to thank Mrs. V. Glooschenko, Dr. P. Keddy, and Ms E. Bottomley for criticisms of a draft manuscript and Dr. D. Busch, Dr. W. Flint, Dr. T. Stephenson, and Dr. T. Whillans for helpful discussions. We should also like to thank the members of Project Quinte and our other collaborators in research.

References

ANONYMOUS. 1987. Bass, grass carp and hydrilla. Aquaphyte 7(2): 5.

ARGUS, G. W., AND D. J. WHITE. 1977. The rare vascular plants of Ontario. Natl. Mus. Nat. Sci. (Ottawa) Syllog. 14.

ASHWORTH, W. 1986. The late Great Lakes. Random House, New York, NY. 276 p.

BANNISTER, T. T., AND R. C. BUBECK. 1978. Limnology of Irondequoit Bay, Munroe County, p. 105–221. *In* J. Bloomfield [ed.] Lakes of New York State. Vol. II. Academic Press, New York, NY.

BAYLEY, S., V. D. STOTTS, P. F. SPRINGER, AND J. STEENIS. 1978. Changes in submerged aquatic macrophyte populations at the head of Chesapeake Bay, 1958–1975. Estuaries 1: 73–84.

BEETON, A. M. 1965. Eutrophication of the St. Lawrence Great Lakes. Limnol. Oceanogr. 10: 240–254.

BOTTOMLEY, E. J. Z. 1986. Wetlands and waterfowl of the St. Lawrence River in Ontario: initial baseline study. Canadian Wildlife Service, Ottawa, Ont.

BOTTOMLEY, E. J. Z., T. J. ELLIS, AND D. B. WHITE. 1987. Mapping of submerged aquatic vegetation from satellite data. Proc. Seventh Annual Conference of the Society of Canadian Limnologists, Richmond, B.C.

BUSCH, W-D., N. R. KAVETSKY, AND G. MCCULLOUGH. 1989. Water level criteria for Great Lakes wetlands. Summary. Wetlands Workshop, January 1989, Buffalo, NY. 59 p.

CARTER, V., AND G. M. HARAMIS. 1980. Distribution and abundance of submersed aquatic vegetation in the tidal Potomac River, implications for waterfowl. Atl. Nat. 33: 14–19.

CARTER, V., AND N. B. RYBICKI. 1985. The effects of grazing and light penetration on the survival of aquatic macrophytes. Aquat. Bot. 23(3): 197–213.

CATLING, P. M., AND S. M. MCKAY. 1975. Associations of halophytic plants in the Toronto region. Ont. Field Biol. 29: 50–55.

CECILE, C. P. 1983. Oshawa Second Marsh baseline study. Final Report. Environment Canada, Ottawa, Ont.

CHAMBERS, P. A., AND J. KALFF. 1987. Light and nutrients in the control of aquatic plant community structure. J. Ecol. 75: 611–619.

CHAMBERS, P. A., AND E. E. PREPAS. 1988. Underwater spectral attenuation and its effect on the maximum depth of angiosperm colonization. Can. J. Fish. Aquat. Sci. 45: 1010–1017.

CROWDER, A. A., AND J. M. BRISTOW. 1986. Aquatic macrophytes of the Bay of Quinte: 1972–82, p. 114–127. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86.

1988. The future of waterfowl habitats in the Canadian lower Great Lakes wetlands. J. Great Lakes Res. 14: 115–127.

CROWDER, A. A., J. M. BRISTOW, M. R. KING, AND S. VANDERKLOET. 1977. The aquatic macrophytes of some lakes in southeastern Ontario. Nat. Can. 104: 457–464.

CROWDER, A. A., W. T. DUSHENKO, J. GREIG, AND J. S. POLAND. 1989. Metal contamination in sediments and biota of the Bay of Quinte, Lake Ontario, Canada. Hydrobiologia 188/189: 337–343.

CROWDER, L. B., AND W. E. COOPER. 1979. The effects of macrophyte removal on the feeding efficiency and growth of sunfishes. Evidence from pond studies, p. 251–268. *In* J. E. Breck, R. T. Prentki, and O. L. Loucks [ed.] Aquatic plants, lake management, and ecosystem consequences of lake harvesting. Conf. Proc., 14–16 February 1979, Madison, WI.

CURTIS, S. G., D. G. DENNIS, AND H. BOYD [ED.] 1984. Wildlife studies in Ontario 1973–81. Can. Wildl. Serv. Occas. Pap. No. 54.

DICKMAN, M., C. PRESCOTT, AND K. L. E. KAISER. 1983. Variations in the aquatic vegetation of the Welland River (Ontario, Canada) above and below an industrial water discharge. J. Great Lakes Res. 9: 317–325.

DUARTE, C. M., AND J. KALFF. 1988. Influence of lake morphometry on the response of submerged macrophytes to sediment fertilization. Can. J. Fish. Aquat. Sci. 45: 216–221.

DUSHENKO, W. 1990. Physical and chemical factors affecting nearshore aquatic vegetation in the Bay of Quinte, Lake Ontario, Ph.D. thesis, Queen's University, Kingston, Ont.

DUSHENKO, W. T., A. CROWDER, AND B. CAMERON. 1990. Revegetation in the Bay of Quinte, Lake Ontario: preliminary lab and field experiments. Int. Symp. Wetland Managers, Niagara Falls, Ont.

DUSHENKO, W., A. CROWDER, AND J. GREIG. 1989. Shoreline distribution of contaminants and submerged macrophytes in the Bay of Quinte, Ontario, p. 377–384. *In* M. J. Bardecki and N. Patterson [ed.] Ontario wetlands: inertia or momentum. Federation of Ontario Naturalists, Don Mills, Ont.

EDSALL, T. A., B. A. MANNY, AND C. N. RAPHAEL. 1988. The St. Clair River and Lake St. Clair, Michigan: an ecological profile. Natl. Fish Res. Centre — Great Lakes. Contrib. 682. U.S. Fish and Wildlife Service, Ann Arbor, MI.

ENGEL, S. 1987. The impact of submerged macrophytes on largemouth bass and bluegills. Lake Reservoir Manage. 3: 235–242.

ENVIRONMENT CANADA, CANADIAN WILDLIFE SERVICE, AND U.S. DEPARTMENT OF INTERIOR, FISH AND WILDLIFE SERVICE. 1986. North American Waterfowl Management Plan. (Available from the Canadian Wildlife Service, Environment Canada, Ottawa, Ont. K1A 0H3)

ERICHSON, D. W., AND J. S. LINDZEY. 1983. Lead and cadmium in muskrat and cattail tissues. J. Wildl. Manage. 47: 550–555.

EVERETT, J. J., AND R. G. ANTHONY. 1976. Heavy metal accumulation in muskrats in relation to water quality. Fish Wildl. Conf. 33: 105–116.

FISHERIES AND ENVIRONMENT CANADA AND ONTARIO MINISTRY OF NATURAL RESOURCES. 1979. Shore property hazards. 14 p. (Available from Information Services Branch, Ontario Ministry of Natural Resources, Whitney Block, 99 Wellesley St. W., Toronto, Ont. M7A 1W3, Canada)

FOREST, H. 1987. The remarkable recovery of submerged vegetation in Irondequoit Bay. Bull. 296, Rochester Committee for Scientific Information, Rochester, NY.

FULLER, D. A., C. E. SASSER, W. B. JOHNSON, AND J. G. GOSSELINK. 1984. The effects of hebivory on vegetation on islands in the Atchafalaya Bay, Louisiana. Wetlands 4: 105–114.

GEIS, J. W. 1985. Environmental influences on the distribution and composition of wetlands in the Great Lakes Basin, p. 15–31. *In* H. H. Prince and F. M. D'Itri. [ed.] Coastal wetlands. Lewis Publishers, Chelsea, MI.

GEIS, J. W., AND J. L. KEE. 1977. Coastal wetlands along Lake Ontaio and the St. Lawrence River in Jefferson County, New York. Wisc. Acad. Sci. Arts Lett. 24.

GERRISH, N., AND J. M. BRISTOW. 1979. Macroinvertebrate associations with aquatic macrophytes and artificial substrates. J. Great Lakes Res. 5: 69–72.

GLOOSCHENKO, V., B. PARKER, C. COO, R. KENT, C. WEDELES, A. MASON, J. DAWSON, D. HERMAN, AND P. SMITH. 1987. Provincially and regionally significant wetlands in southern Ontario. Interim report. Ontario Ministry of Natural Resources, Toronto, Ont.

GLOOSCHENKO, W. A. 1978. Sedimentary geochemistry of a Lake Ontario urban marsh, p. 63–64. *In* N. A. Rukavina [ed.] Proceedings of 2nd Workshop on Great Lakes Coastal Erosion and Sedimentation. CCIW, Burlington, Ont.

GREIG, J. 1989. Distribution of selected elements in substrates, plants and snails from marshes in the Bay of Quinte, Ontario. M.Sc. thesis, Queen's University, Kingston, Ont

GREIG, J., W. T. DUSHENKO, A. CROWDER, AND J. POLAND. 1989. Contaminants in biota and sediments in shoreline habitats of the Bay of Quinte, Lake Ontario. Environmental Research, Technology Transfer Conference, Nov. 1989, Toronto, Ont. I: 292–301.

HAMILTON, P. B., AND L. WILSON-NEISH. 1988. The occurrence of freshwater and red algae in Ontario. The Plant Press 5(1): 11–15.

JOHNSON, M. G., AND R. O. BRINKHURST. 1971. Associations and species diversity in benthic macroinvertebrates of Bay of Quinte and Lake Ontario. J. Fish. Res. Board Can. 28: 1683–1697.

KEAST, A. 1984. The introduced aquatic macrophyte *Myriophyllum spicatum* as habitat for fish and their invertebrate prey. Can. J. Zool. 62: 1289–1303.

KELLEY, J. C., T. M. BURTON, AND W. R. ENSLIN. 1985. The effects of natural water level fluctuations on N and P cycling in a Great Lakes marsh. Wetlands 4: 159–175.

KEOUGH, J. K. 1986. The Mink River — a freshwater estuary. Wisc. Acad. Sci. Arts Lett. 24: 1–11.

KORSCHGEN, C. E., L. S. GEORGE, AND W. L. GREEN. 1988. Feeding ecology of canvasbacks staging on Pool 7 of the Upper Mississippi River, p. 237–249. *In* M. W. Weller [ed.] Proc. Waterfowl in Winter Symposium, Galveston, TX.

LES, D., J. KEOUGH, G. GUNTENSPERGEN, AND F. STEARNS. 1988. Feasibility of increasing macrophyte diversity in Lac la Belle and Okauchee Lake, Waukesha County, Wisconsin, U.S.A. Department of Biological Science, University of Wisconsin Milwaukee, Milwaukee, WI.

LESLIE, A. J., J. M. VANDYKE, R. S. HESTAND, AND B. Z. THOMPSON. 1987. Management of aquatic plants in multi-use lakes with grass carp (*Ctenopharyngodon idella*). Lake Reservoir Manage. 3: 266–276.

LIMNOS LTD. 1989. Distribution, species composition and biomass of macrophytes in the Bay of Quinte. A comparison of methodologies. Limnos Ltd., Toronto, Ont. 56 p.

MCLARTY, A. W., AND A. G. THACHUK. 1986. Coote's Paradise study. Ontario Ministry of the Environment, Water Resources Assessment Unit Technical Support Section, West Central Region, Hamilton, Ont.

MINNS, C. K., D. A. HURLEY, AND K. H. NICHOLLS [ED.] 1986. Project Quinte: point source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86.

MOLL, D. 1985. The trophic ecology of aquatic turtles: investigations of the relationship of prey availability with dietary overlap and specialization. ASRA J. 2(4): 2–22.

MUDROCH, A. 1981. A study of selected Great Lakes coastal marshes. Sci. Ser. No 122. Inland Waters Directorate, National Water Research Institute, Burlington, Ont. 44 p.

MUDROCH, A., L. SARAZIN, AND T. LOMAS. 1988. Summary of surface and background concentrations of selected elements in the Great Lakes sediments. J. Great Lakes Res. 14: 241–251.

OGLESBY, R. T. 1978. The limnology of Cayuga Lake, p. 2–121. *In* J. A. Bloomfield [ed.] Lakes of New York State. Vol. I. Academic Press, New York, NY.

OLIVER, D. R. 1984. Description of a new species of *Cricotopus* van der Wulp (Diptera: Chironomidae) associated with *Myriophyllum spicatum*. Can. Entomol. 116: 1287–1292.

PAINTER, D. S., AND G. KAMAITIS. 1985. Reduction of *Cladophora* biomass and tissue phosphorus in Lake Ontario, 1972–1983. No. 85-539, National Water Research Institute, Canada Centre for Inland Waters, Burlington, Ont.

PAINTER, D. S., AND K. J. MCCABE. 1988. Investigation into the disappearance of eurasian watermilfoil from the Kawartha Lakes. J. Aquat. Plant Manage. 26: 3–12.

PAINTER, D. S., K. J. MCCABE, AND W. L. SIMSER. 1988. Past and present limnological conditions in Coote's Paradise affecting aquatic vegetation. National Water Research Institute Contrib. 88-47, Burlington, Ont.

PATTERSON, N. J., AND T. H. WHILLANS. 1985. Human interference with natural waterlevel regimes in the context of other cultural stresses on Great Lakes wetlands. p. 209–239. *In* H. H. Prince and F. M. D'Itri [ed.] Coastal wetlands. Lewis Publishers, Chelsea, MI.

POWLES, P. M., H. R. MACCRIMMON, AND D. A. MACRAE. 1983. Seasonal feeding of carp *Cyprinus carpio*, in the Bay of Quinte water shed. Can. Field-Nat. 97: 293–298.

QUINLAN, C., AND G. MULAMOOTIL. 1987. The effects of water level fluctuations on three Lake Ontario shoreline marshes. Can. Water Res. 12: 64–77.

RUTA, P. 1981. Littoral macrophyte communities of the St. Lawrence River, New York. M.Sc. thesis, State University of New York, Syracuse, NY.

RYBICKI, N. B., AND V. CARTER. 1986. Effect of sediment depth and sediment type on the survival of *Vallisneria americana* Michx, grown from tubers. Aquat. Bot. 24: 233–240.

SCHLOESSER, D. W., P. L. HUDSON, AND S. J. NICHOLS. 1986. Distribution and habitat of *Nitellopsis obtusa* (Characeae) in the Laurentian Great Lakes. Hydrobiologia 133: 91–96.

SCHWARTZ, L. N., AND G. K. GRUENDING. 1986. The effects of sewage on a Lake Champlain wetland. J. Freshwater Ecol. 3: 35–46.

SHEATH, R. G., AND K. M. COLE. 1980. Distribution and salinity adaptations of *Bangia atropurpurea* (Rhodophyta), a putative migrant into the Laurentian Great Lakes. J. Phycol. 16: 412–420.

SMART, G. C., K. GERBER, AND R. J. COX. 1987. Nematodes as biological agents for aquatic weeds. Aquaphyte 7(1): 5–6.

SPENCER, C. N., N. R. KEVERN, AND T. M. BURTON. 1984. The role of wetlands in nutrient cycling in the Great Lakes region. Research for Managing the Nation's Estuaries. Conf. Proc. (Raleigh, NC) Sea Grant Publ. 84-08: 177–201.

STEPHENSON, T. D. 1989. Significance of Toronto area coastal marshes for fish, p. 415–423. *In* M. J. Bardecki and N. Patterson [ed.] Ontario wetlands: inertia or momentum. Federation of Ontario Naturalists, Don Mills, Ont.

TOWNSEND, P. F. 1979. Some dietary and ecological considerations of the common snapping turtle in Delaware. Bull. Md. Herpetol. Soc. 15: 65–69.

VALENTINE, J. M. 1978. Plant succession after sawgrass mortality in S. W. Louisiana, p. 634–640. *In* W. Rogers [ed.] 30th Annual Conference S.E. Association of Fish and Wildlife Agencies, New Orleans, LA.

WESELOH, D. V., J. STRUGER, R. TURTLE, A. SCHEUHAMMER, AND H. WON. 1987. The use of Pekin ducks as *in situ* indicators of Great Lakes organochlorine and metal contamination, p. A-61. *In* Abstr. Int. Assoc. Great Lakes Res. 30th Conf., May 1987, Ann Arbor, MI.

WETZEL, R. 1990. Nutrient retention by wetlands. Great Lakes Wetlands 1: 3, 5.

WHILLANS, T. H. 1989. Wetlands and fisheries in central Ontario lakes, p. 407–414. *In* M. J. Bardecki and N. Patterson [ed.] Ontario wetlands: inertia or momentum. Federation of Ontario Naturalists, Don Mills, Ont.

Changes in the Nearshore and Offshore Zooplankton Communities in Lake Ontario: 1981–88[1]

Ora E. Johannsson

Department of Fisheries and Oceans, Great Lakes Laboratory for Fisheries and Aquatic Sciences, Canada Centre for Inland Waters, 867 Lakeshore Rd., Burlington, Ont. L7R 4A6, Canada

Edward L. Mills

Cornell University Biological Field Station, 900 Shackleton Point Rd., Bridgeport, NY 13030-9750, USA

and Robert O'Gorman

United States Fish and Wildlife Service, Oswego Biological Station, 17 Lake Street, Oswego, NY 13126, USA

Johannsson, O. E., E. L. Mills, and R. O'Gorman. 1991. Changes in the nearshore and offshore zooplankton communities in Lake Ontario: 1981–88. Can. J. Fish. Aquat. Sci. 48: 1546–1557.

We examined trends and factors influencing changes in nearshore and offshore zooplankton abundance and composition in Lake Ontario between 1981 and 1988. In the nearshore (southshore and eastern basin), zooplankton abundance decreased and shifts occurred in the relative abundances of *Bosmina longirostris* and *Daphnia retrocurva* (eastern basin) and *Daphnia retrocurva* and *Daphnia galeata mendotae* (southshore). These changes could have resulted from increased vertebrate predation or reduced food resources which intensified the effects of predation. In the offshore, the first appearance (FA) of the larger, less common cladoceran species occurred earlier in the season as of 1985. FA was correlated with cumulative epilimnetic temperature (CET) and the catch per unit effort (CPUE) of alewife (*Alosa pseudoharengus*) ≥165 mm caught in U.S. waters in the spring. In 1987, when CET was high and CPUE of alewife ≥165 mm was low, large populations of these cladocerans developed in June and July. *Bythotrephes cederstroemi*, a recent invader in the Great Lakes, was abundant only in 1987 when the CPUE of alewife was lowest. Changes in zooplankton abundance, development, and composition along the nearshore–offshore gradient reflected effects of temperature, habitat, and planktivory on the community.

Les auteurs ont étudié les tendances et les facteurs qui ont influé sur les variations, entre 1981 et 1988, de l'abondance et de la composition du zooplancton des eaux côtières et hauturières du lac Ontario. Dans les eaux côtières (soit le littoral sud et le bassin oriental), l'abondance du zooplancton a diminué et des variations de l'abondance relative ont été notées dans le cas de *Bosmina longirostris* et *Daphnia retrocurva* (bassin oriental) et de *Daphnia retrocurva* et *Daphnia galeata mendotae* (littoral sud). Ces variations peuvent être le résultat d'une prédation plus intense de la part de vertébrés ou d'une pénurie de ressources alimentaires qui ont intensifié les incidences de la prédation. Dans les eaux hauturières, les espèces de cladocères moins communes et de grande taille ont été relevées pour la première fois plus tôt au cours de la saison dès 1985. Cette première observation était en corrélation avec la température cumulative de l'épilimnion (CET) et les prises par unité d'effort (PUE) de gaspareau (*Alosa pseudoharengus*) de longueur égale ou supérieure à 165 mm capturé dans les eaux américaines au cours du printemps. En 1987, lorsque la CET était élevée et que les PUE de gaspareau de cette taille étaient faibles, d'importantes populations de ces cladocères ont été relevées en juin et juillet. *Bythotrephes cederstroemi*, une espèce qui a récemment envahi les Grands Lacs, n'était abondante qu'en 1987 lorsque les PUE de gaspareau étaient à leur plus faible niveau. Les variations de l'abondance, de la composition et de la prolifération du zooplancton le long du gradient côtier–hauturier traduisent les incidences de la température, de l'habitat et de la planctophagie sur la communauté.

Received May 25, 1989
Accepted March 13, 1991
(JA178)

Reçu le 25 mai 1989
Accepté le 13 mars 1991

The zooplankton of Lake Ontario were not studied systematically until the late 1960's – early 1970's. Whole-lake or large-scale studies from 1967 to 1972 (Patalas 1969; McNaught and Buzzard 1973; Czaika 1974; Watson and Carpenter 1974) found that the zooplankton community was composed of small cladocerans and cyclopoids, principally *Diacyclops thomasi*, *Bosmina longirostris*, and *Daphnia retrocurva*. This community was still present in the early 1980's (Johannsson 1987; Taylor et al. 1987). The predominance of such small species is characteristic of planktivore-dominated systems where the fish feed selectively on larger individuals (Mills and Schiavone 1982; McQueen et al. 1986; Mills et al. 1987; Post and McQueen 1987; McQueen and Post 1988). Alewife (*Alosa pseudoharengus*) are the most abundant planktivores in the lake (O'Gorman et al. 1987b) and are confined largely to the epilimnion during summer thermal stratification (Olson et al. 1988). Their abundance varies from year to year

[1]Contribution No. 107 of the Cornell University Biological Field Station, Bridgeport, NY 13030-9750, USA, and Contribution No. 764 of the National Fisheries Research Center – Great Lakes, Ann Arbor, MI 48105, USA

in Lake Ontario and annual differences are reflected in certain changes in the mean size, abundance, productivity, and egg ratio of the dominant epilimnetic cladocerans (Johannsson and O'Gorman 1991).

Zooplankton are the pivotal trophic level in lake ecosystems, responding to both "top-down" and "bottom-up" forces (McQueen et al. 1986) as well as to environmental conditions (Patalas 1969, 1972). In Lake Ontario, nutrient levels and alewife abundance have changed or fluctuated during the 1980's, and these changes have likely influenced the composition and abundance of the zooplankton community. Nitrate has increased, while spring total phosphorus has decreased (Stevens and Neilson 1987; International Joint Commission 1989). Summer total phosphorus concentrations in the epilimnion appear to be governed by summer tributary inputs (Neilson and Stevens 1987) and did not experience the same rate or pattern of decrease as did spring total phosphorus levels (Stevens and Neilson 1987). In the main lake and eastern basin, summer epilimnetic phosphorus concentrations were lower during 1987–89 than during 1981–86 (Johannsson et al. 1991). Alewife abundance has fluctuated in response to climatic changes (O'Gorman et al. 1987b), and perhaps more subtly to the stocking of salmonids.

In the present study, we examine trends and factors influencing changes in both the nearshore and offshore zooplankton communities in Lake Ontario between 1981 and 1988.

Methods and Materials

Zooplankton samples were collected under two, independent monitoring programs. One program was operated by Cornell University, the U.S. Fish and Wildlife Service, and the New York State Department of Environmental Conservation and the other by the Canadian Department of Fisheries and Oceans.

In U.S. waters, zooplankton were collected at 4- to 6-wk intervals from April through October from four sites in 1986 and 1987 (Fig. 1). During 1984–88, they were also sampled at four sites along a transect off Nine Mile Point in late July – early August (Fig. 1). Sites were located 2 and 20 km from shore off Oak Orchard and Smoky Point. Transect sites were situated at specific depth contours: 15 m (0.7 km from shore), 30 m (1.6 km), 50 m (2.9 km), and 100 m (6.8 km).

Zooplankton were collected by towing a 0.5-m-diameter, 153-μm-mesh nylon net vertically through the water column. Temperatures in the water column were measured with a bathythermograph. If the lake was isothermal, the net was raised from the bottom (2-km site) or from a depth of 50 m (20-km site). If the lake was stratified, zooplankton were collected from the top of the thermocline to the surface, except in 1984 and 1985 when the 50-m (2.9 km) and 100-m (6.8 km) stations at Nine Mile Point were sampled to the bottom. Zooplankton were preserved in a sugar–formalin solution (Haney and Hall 1973) immediately after they were rinsed from the net. In the laboratory, zooplankton were identified and counted as outlined in Mills and Confer (1986).

In Canadian waters, zooplankton samples were collected weekly (April–October) from two stations, one midlake 28 km off the north shore (station 41) and one in the centre of the eastern basin 8 km north of Main Duck Island (station 81) (Fig. 1). In 1981 and 1982, 0.25- and 0.30-m-diameter, 64-μm-mesh nylon nets were used to sample zooplankton. In 1983, net diameter was increased to 0.5 m. The original 0.25- and 0.30-m-diameter nets had been lost; therefore, the efficiencies of the three nets could not be compared. Before sam-

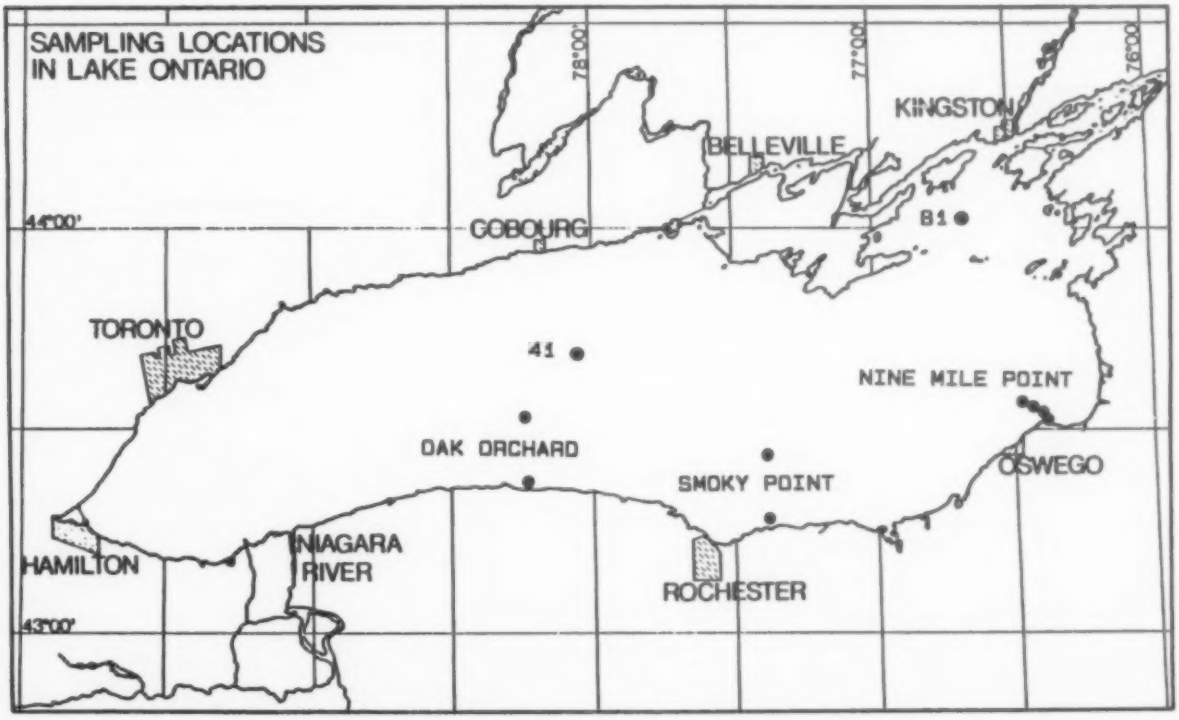


FIG. 1. Map of Lake Ontario showing locations of zooplankton sampling stations.

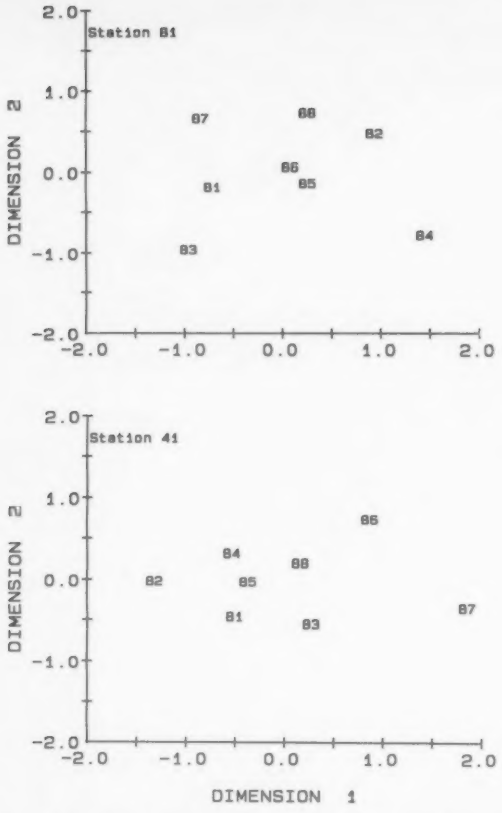


FIG. 2. Relationships amongst years revealed by multidimensional scaling of zooplankton communities at stations 41 and 81. Correlations: station 81: dimension 1 - *Leptodora* (−0.526), *Tropocyclops* (−0.563); dimension 2 - *Leptodora* (−0.690), *Tropocyclops* (−0.645), *Mesocyclops* (−0.789), *Bosmina* (−0.809)/*Holopedium* (0.661); station 41: dimension 1 - *D. g. mendotae* (0.728), *Polyphemus* (0.792)/*Bosmina* (−0.660), total cladocerans (−0.642); dimension 2 - *Eurytemora* (0.718)/*Eubosmina* (−0.541).

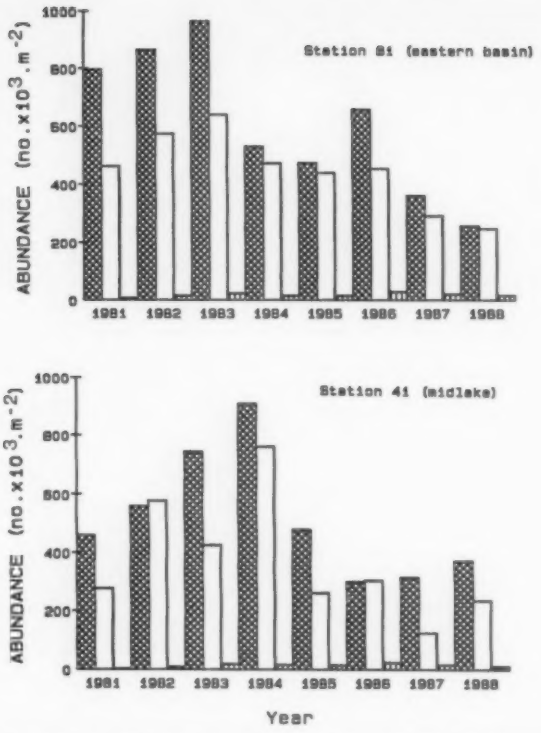


FIG. 3. Mean epilimnetic abundances of copepods (■), cladocerans (□), and calanoids (▩) at two stations, eastern basin and midlake, in Lake Ontario during June–October 1981–88. Each estimate is based on 19–21 samples collected at weekly intervals through the season. The samples were weighted by the true sample intervals to minimize the effect of missing data.

pling the zooplankton, we determined temperatures in the water column with an electronic bathythermograph. During unstratified and deeply stratified conditions, samples were collected from 20 m to the surface. When stratification was less than 20 m, samples were taken from 1 m above the thermocline to the surface. Zooplankton were preserved in 4% sugared formalin and later identified and counted with a stratified counting regime (Cooley et al. 1986). The Cladocera and adult Copepoda were identified to species and the copepodids and nauplii to Order. Epilimnetic abundances (number per square metre) were calculated by multiplying density by sample depth. Abundances were weighted by the sample interval and then averaged over the June–October period in order to compare abundance across years.

The temperature profile was averaged through the depth of the epilimnion in order to calculate mean epilimnetic temperature. Because growth of zooplankton is related to temperature (Patalas 1969; Johannsson 1987) and because we needed a measure of the "growth potential" of the environment at our midlake site during the early summer, we calculated the cumulative epilimnetic temperature at station 41 for each year: this measure is equivalent to degree-days. In order to exclude periods of the year when waters were too cold to support summer populations, we started the accumulation when epilimnetic temperatures reached 10°C and stopped on July 31.

Alewife were assessed with bottom trawls in U.S. waters by the U.S. Fish and Wildlife Service and the New York State Department of Environmental Conservation during late April – early May 1980–89. Survey methods were described by O'Gorman and Schneider (1986) and O'Gorman et al. (1897b) and are reviewed here only briefly. Trawls were fished along 12 transects spaced roughly 28 km apart from Olcott, New York (29 km east of the Niagara River mouth), to Cape Vincent, New York (at the head of the St. Lawrence River). Range of bottom depths fished was 8–150 m and, on average, 103 trawl tows were made each year (range 75–122). Standard tows were of 10-min duration and were made along the contour at 4.6 km·h^{-1}.

Our measure of alewife abundance was a stratified catch per standard trawl tow (CPUE). It was calculated by first dividing U.S. waters into seven strata. Stratification was by depth and was appropriate because of large, consistent differences between catches at different depths. Then we assumed that our catches constituted a stratified random sample and calculated the stratified CPUE accordingly.

After a trawl tow, adult alewife (age 2 and older) were sorted and counted separately from yearling alewife. We separated life stages on the basis of length and verified annually that the length used was appropriate by aging a sample of fish. When catches

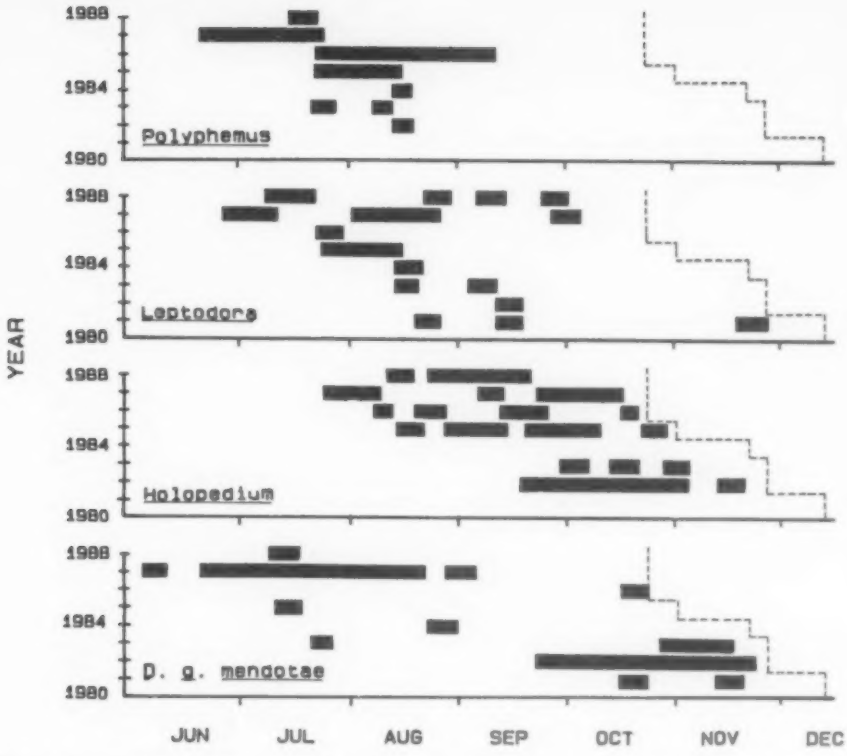


FIG. 4. Time periods (solid bars) when four secondary cladocerans were found at station 41, midlake, Lake Ontario. Broken lines represent the end of the sampling season.

TABLE 1. Cumulative epilimnetic temperature (CET) calculated from the time the epilimnion reached 10°C until July 31, and the stratified catch per tow (CPUE) of alewife ≥165 mm in bottom trawls fished in U.S. waters each spring. FA is the average date of first appearance of *L. kindtii*, *P. pediculus*, *H. gibberum*, and *D. g. mendotae* at station 41, expressed in Julian days.

Year	CET (°C)	Alewives ≥165 mm (CPUE)	FA
1981	827	1220	251
1982	615	1162	250
1983	850	1188	223
1984	741	646	225
1985	731	668	210
1986	649	536	230 (207)[a]
1987	1027	184	177
1988	746	415	199

[a]The value in parentheses does not include *D. g. mendotae*. it occurred very late in 1986, while the other three species were early.

were large (greater than 75 kg), species and life stages in a random subsample were counted and weighed; the rest of the catch was weighed in aggregate and composition was estimated by direct proportion.

We separated life stages because the CPUE of adult alewife was a good index of adult abundance during summer whereas the CPUE of yearling alewife was not a good index of yearling abundance during summer. Survival of alewife from age 1 to age 2 is highly variable in Lake Ontario (O'Gorman et al. 1987b). Furthermore, O'Gorman et al. (1987b) argued that

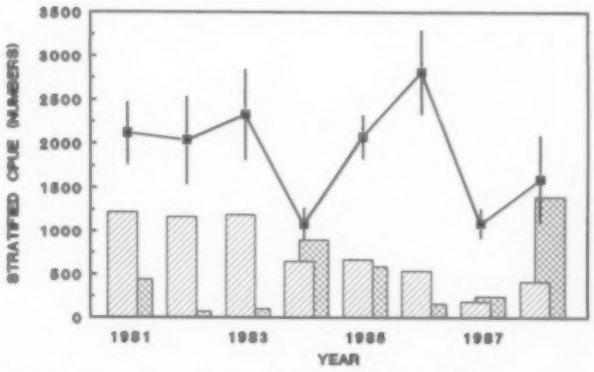


FIG. 5. Stratified catch per trawl tow (CPUE) of various groups of alewife in the US waters of Lake Ontario, 1981–88. CPUE of age-2 and older alewife (± 1 SE) (■) was calculated from catches of spring bottom trawls; abundance of alewife ≥165 mm (▩) is their proportional contribution to the CPUE of alewife age-2 and older, estimated by random length sampling of the spring alewife catches; abundance of age-1 alewife (▩) is the CPUE of age-2 alewife the following spring estimated from random length sampling and an age–length key.

most yearling mortality occurs in spring, when age-1 and adult alewife are nearshore. Their argument is bolstered by the positive correlation between weight of mature coho salmon (*Oncorhynchus kisutch*) in the fall (1977–82) and the biomass of age-2 alewife the following spring ($r = +0.98, P < 0.01$).

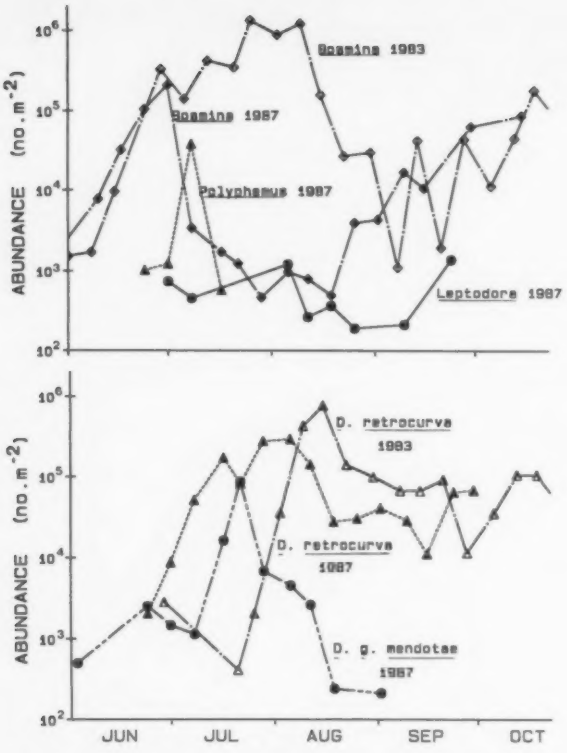


FIG. 6. Seasonal development of *D. retrocurva* and *B. longirostris* populations at station 41 (midlake) in 1987 and 1983, the next warmest year. In 1983, *P. pediculus* was seen twice (Fig. 4): in late July at 4100·m^{-2} and in early August at 4500·m^{-2}. $N = 1$.

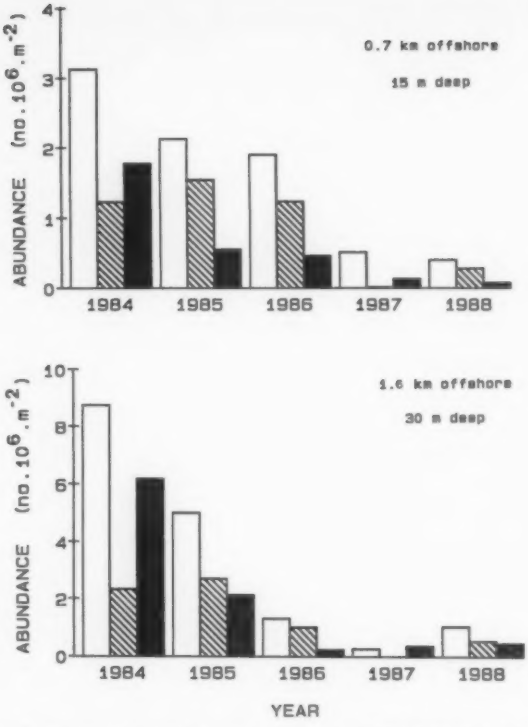


FIG. 7. Changes in zooplankton abundance near Nine Mile Point, Lake Ontario, 1984–88. Samples were collected 0.7 and 1.6 km from shore (15 and 30 m bottom depth) once each year between July 18 and August 4. □, total zooplankton; ▨, *B. longirostris*, ■, *D. thomasi*.

The correlation strongly suggests that abundance of age-2 alewife in spring was an accurate index of yearling alewife available for the coho salmon to eat the previous summer. Accordingly, for an index of yearling abundance, we used CPUE of age-2 alewife the following spring.

Age composition was determined by applying age–length keys constructed from aged samples of 500–800 alewife to much larger samples of lengths. Ages were determined from scales during 1981–83 and from otoliths thereafter. The change was prompted by the observation that otoliths yielded more accurate (older) ages for alewife in the Great Lakes (O'Gorman et al. 1987a).

To determine length composition, we recorded total lengths (millimetres) at six transects each spring. All adult alewife in a small catch (generally 100 adults or less) and in a random sample from large catches were measured. The random sample was used to estimate the number of adult alewife in each 5-mm length group in that trawl haul. Length data from all trawl hauls and transects were summed to obtain a length–frequency distribution. We measured 3600–6400 adult alewife each spring. The CPUE for a length group or an age group was the same proportion of the total CPUE as that which the group contributed to the total length–frequency distribution or age composition.

Data Analysis

We tried to examine the lake as a whole, although the data were collected quite differently by the two monitoring programs. Because differences in the mesh sizes of the nets (153 versus 64 μm) and sampling-depth protocols of the two programs would affect sampling efficiencies and abundance estimates, we examined each data set separately, and only compared trends between the data sets. None of the data reported here are for metered nets. The 64-μm-mesh nets were metered in the later years of this study and had an average efficiency of 55%. The efficiency was lowest in May during the diatom bloom (approximately 40%) and highest in July and August during summer stratification when cladocerans were abundant (approximately 70%).

We assessed the midlake (station 41) and eastern basin (station 81) zooplankton communities for structural changes during the 1980's by applying multidimensional scaling techniques (Wilkinson 1988) to the matrix of community similarity values. For each station, for each pair of years, the matrix contained a single seasonal estimate of community similarity, calculated by applying the seasonal (dis)similarity index (Johannsson and Minns 1987). The index can use any measure of community similarity: we employed percentage similarity (Gauch 1982, p. 112). In order to interpret the resulting scalar scores, we determined their correlations with temperature and the average abundances of the zooplankton species.

Nearshore–offshore and seasonal changes in the US zooplankton community at Oak Orchard and Smoky Point were investigated with factor analysis (Wilkinson 1988). We first determined the percentage composition of species in each of the monthly samples from all years and then plotted the distribution of percentages for the untransformed, and arcsin and

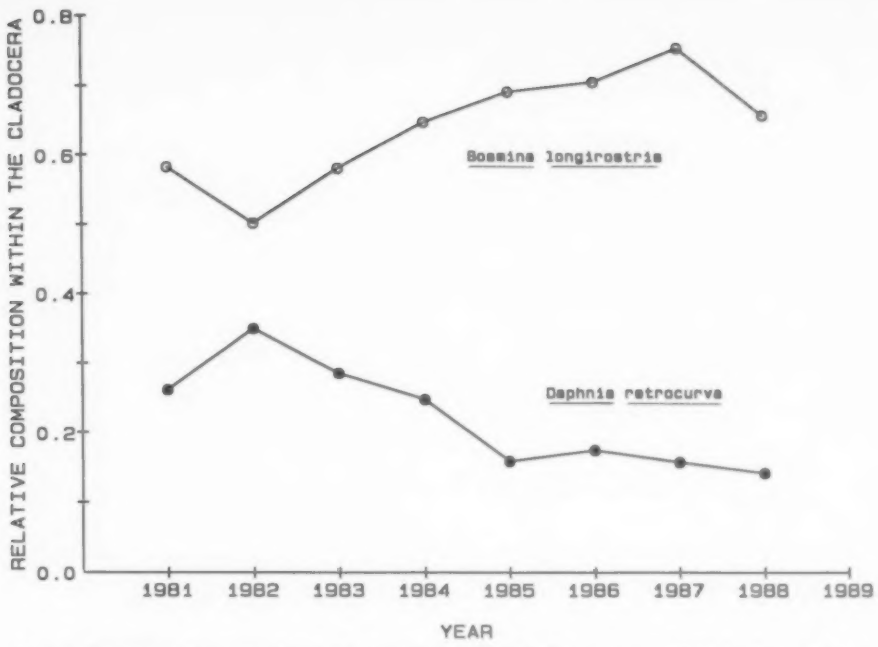


FIG. 8. Changes in the proportions of *B. longirostris* (○) and *D. retrocurva* (●) in the June–October cladoceran community at station 81 in the eastern basin, Lake Ontario, 1981–88.

$\ln(x + 0.0001)$ transformed data, for each species. Because all copepod nauplii were lumped in the species count, they were treated as a species in these analyses. Because the distributions of species with large numbers of zeros (not present) remained highly skewed, these species were dropped from the analysis. The ln-transformed percentages most closely approximated normal distributions in all seven remaining species/group, except *Diacyclops thomasi*: i.e. *B. longirostris, D. retrocurva, Tropocyclops prasinus, Diaptomus oregonensis, Diaptomus minutus*, and nauplii. Therefore, all percentages were ln transformed, except that of *D. thomasi*, and then standardized in preparation for factor analysis. The axes were rotated by use of varimax rotation, then the factor scores were estimated for each sample, and finally, the correlation matrix relating factor scores and species percent composition was calculated. The significance of trends in abundance across years was evaluated by use of the sign test (Siegel 1956).

Results and Discussion

Overall Fluctuations in Composition and Abundance

The zooplankton community in Lake Ontario between 1981 and 1988 was dominated by *B. longirostris, D. retrocurva, Ceriodaphnia lacustris, Eubosmina coregoni, D. thomasi*, and *T. prasinus*. Multidimensional scaling of the seasonal similarity matrices for stations 41 and 81 over this 8-yr period did not reveal any trend indicating change in zooplankton community composition between 1981 and 1988 (Fig. 2). At station 81, all years fell within ±1.4 scalar units, and no one year was distinctly separate from all the others. At station 41, more range in variability occurred along the first dimension, with 1987 at the far right of the axis. The abundance of *Daphnia galeata mendotae* and *Polyphemus pediculus* were positively correlated with this dimension, while the abundances of *B. longirostris* and total cladocerans were negatively correlated with it.

Johannsson (1987) and Taylor et al. (1987) compared the zooplankton community in Lake Ontario in the early 1980's (1981–84) with those in the late 1960's and early 1970's (Patalas 1969; Watson and Carpenter 1974; Czaika 1974). They found no significant changes in composition or abundance. By the late 1980's, zooplankton composition, with the exception of the midlake in 1987, still had not changed. However, zooplankton abundance decreased during the 1980's. The sign test indicated that total zooplankton abundances at both stations 41 ($p = 0.038$) and 81 ($p = 0.002$) had changed between 1981 and 1988. In the eastern basin, copepod abundance decreased as of 1984, with some temporary recovery in 1986 (Fig. 3). Cladoceran abundances were lower in 1987 and 1988 than in other years (Fig. 3). At station 41 in the midlake, total zooplankton abundance was greatest from 1982 to 1984 (1144×10^3 to $1683 \times 10^3 \cdot m^{-2}$) and lowest from 1986 to 1988 (453×10^3 to $624 \times 10^3 \cdot m^{-2}$) (Fig. 3).

In general, although composition has not changed systematically or substantially through the 1980's, zooplankton abundance has declined as of 1983–84, particularly in the eastern basin.

Offshore Zooplankton Community

Three changes or events were noted in the offshore community during this study. The first was the appearance of the less-abundant, larger cladocerans, such as *Leptodora kindtii, D. g. mendotae, P. pediculus*, and *Holopedium gibberum*, earlier in the season during 1985–88 than during 1981–84 (Fig. 4). Seasonal timing of zooplankton populations can be influenced

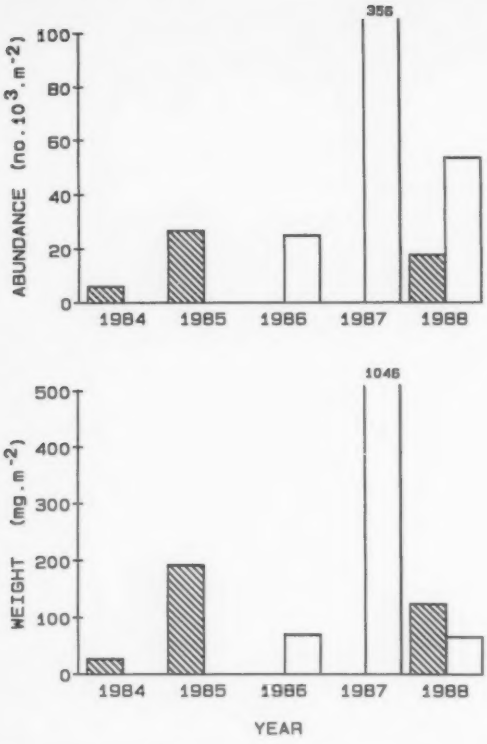


FIG. 9. Species and abundances of *Daphnia* near Nine Mile Point, Lake Ontario, 1984–88: *D. retrocurva* (□) and *D. g. mendotae* (▨). Abundance of daphnids is the average of four net hauls, one each at 0.7, 1.6, 2.9, and 6.8 km from shore. *Daphnia galeata mendotae* was not found in samples of the whole water column at 50 or 100 m in 1984 or 100 m in 1985 and therefore was not in the epilimnion. This permitted calculation of whole-transect averages for these years as well as for years when only the epilimnion was sampled.

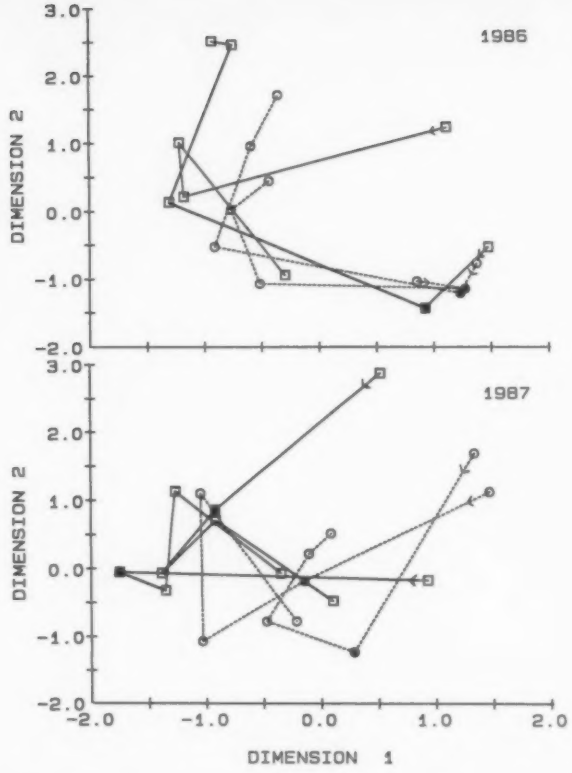


FIG. 10. Seasonal development (April–October) of the zooplankton community in the nearshore (□) and offshore (○) at Oak Orchard and Smoky Point, southshore of Lake Ontario, as revealed by factor analysis. June (spring) is represented by solid symbols. Dimension 1 was correlated with *B. longirostris* (−0.738), *D. retrocurva* (−0.821), *D. minutus* (0.770), nauplii (0.743), *D. oregonensis* (0.660), and *D. thomasi* (0.637). Dimension 2 was correlated with *T. prasinus* (−0.810).

by the rate of warming of the water column (Johannsson 1987), and the average time of first appearane (FA, expressed in Julian days) of the four cladoceran species was weakly correlated with cumulative epilimnetic temperature (CET) ($r = -0.63$) (Table 1). Predation is another factor which could affect FA, especially in a planktivore-dominated system such as Lake Ontario. Predation could operate directly through the planktivore or indirectly through effects of the planktivore on invertebrate predators or zooplankton distribution. Alewife are the dominant epilimnetic planktivores in the lake (see the introduction), while mysids are the only abundant, large invertebrate predator (Carpenter et al. 1974; Watson and Carpenter 1974). *Mysis relicta* eats zooplankton, but consumption of larger species such as *Leptodora* and *Holopedium* has not been documented (Grossnickle 1982). At night, mysids feed in the water column, including the metalimnion, but temperature barriers exclude them from the epilimnion (Beeton 1960). Consequently, they would affect only the metalimnetic portion of any zooplankton population. There is no evidence that any of the four cladoceran species was abundant in the metalimnion in the past when alewife were abundant in the lake (Patalas 1969; Wilson and Roff 1973), nor were they abundant in the metalimnion in 1982 (D. R. S. Lean, H. Frikker, and A. Abbott, National Water Research Institute, Department of the Environment, Burlington, Ont., unpubl. data) or 1986 (O. E. Johannsson, unpubl. data). Invertebrate predation or changes in zooplankton vertical distribution would not appear to be of importance in determining FA. Any effect of predation on FA likely occurs directly through the planktivore. The CPUE of adult alewife, age 2 and older, was at or above 1981–84 levels during 1985–88 (Fig. 5), while the CPUE of alewife (≥165 mm) declined from 1983 to 1987, increasing only slightly in 1988 (Fig. 5). The CPUE of alewife (≥165 mm) was significantly correlated with FA ($r = 0.84$) (Table 1). After considering possible causes, the most likely factors influencing the FA of these larger cladocerans in midlake are the abundance of larger alewife and the rate of warming of the epilimnion. However, there are insufficient data at this time to define or test for relationships between FA, CET, and CPUE of larger alewife.

The second change noted in the offshore zooplankton community was that populations of larger cladocerans occurred not only much earlier in the season in 1987, but also in abundances greater than observed in earlier studies (Patalas 1969; Watson and Carpenter 1974) or previously in the present study: *D. g. mendotae* (maximum abundance = 86 000·m^{-2}), *P. pediculus* (38 000·m^{-2}), *H. gibberum* (480·m^{-2}), *L. kindtii*

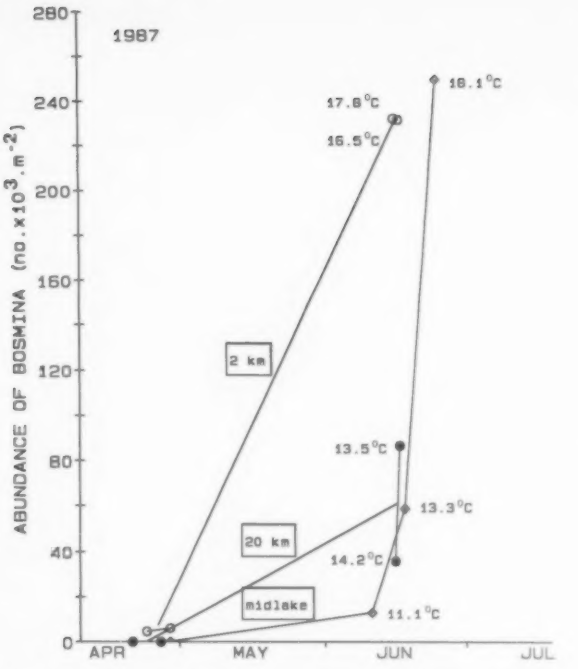


FIG. 11. Abundance of *B. longirostris* in Lake Ontario at various distances from shore in April and June 1987. The 2- and 20-km sites were at Smoky Point and Oak Orchard ($N = 2$), and the midlake site was station 41 ($N = 1$). Water temperature at the time of sampling is given for each sample.

($1200 \cdot m^{-2}$). Numbers of *B. longirostris*, the species that is normally dominant, declined sharply as the *P. pediculus* population expanded (Fig. 6). Because *P. pediculus* can eat *B. longirostris* (Butorina and Sorokin 1966, cited in Champ and Pourriot 1977), there is some question regarding the role of *P. pediculus* in this decline. As discussed above, temperature and predation by alewife are the factors most likely to affect population development of these larger cladocerans. Alewife are thought to move offshore from their inshore spawning sites through late spring and early summer (Wells 1968). However, in 1987 the lake warmed extremely early and rapidly, reaching 10°C on June 3 (Table 1). Unless alewife migration also occurred much earlier than normal, predation in the midlake would be reduced, and populations of larger cladocerans could develop. A decrease in the body size of *D. retrocurva* in early August with the loss of larger individuals suggests that alewife were not abundant midlake until the end of July. A low CPUE of alewife ≥165 mm (Fig. 5) may also have encouraged development of larger cladocerans. However, the relative timing of alewife migration and warming of the water column midlake cannot be dismissed as a possible factor influencing population development of larger cladocerans and zooplankton community structure.

The third change noted was that *Bythotrephes cederstroemi*, a predatory cladoceran which has recently invaded the Great Lakes (Lange and Cap 1986), was observed in both the nearshore and offshore regions in 1987. *Bythotrephes cederstroemi* (Polyphemidae) came to the Great Lakes from Europe and was first reported in Lake Ontario in 1985 along the south shore (Lange and Cap 1986). However, earlier unpublished data of D. R. S. Lean, Hj. Frikker, and A. Abbott (National Water Research Institute, Department of the Environment, Burlington, Ont.) list finding *Bythotrephes* spp. in Lake Ontario in 1982. This is the earliest recording of *Bythotrephes* in the Laurentian Great Lakes and supports the hypothesis of Sprules et al. (1990) that the populations had to be growing undetected in the lakes for some time in order to appear in the abundances first observed in 1985. Comments by Nilsson (1979) suggest that *Bythotrephes* spp. are difficult to sample. He noted that although *B. longimanus* was found abundantly in fish guts in Lake Vanern, it escaped being sampled with plankton nets. Therefore, *B. cederstroemi* has likely been in Lake Ontario since the early 1980's and has only recently been sufficiently abundant to be detected. We found *B. cederstroemi* in September and October of 1987 at all stations. Abundances averaged $145 \cdot m^{-2}$ (station 41), $30.6 \cdot m^{-2}$ (station 81), and $3.2 \cdot m^{-2}$ (US sites). Makarewicz and Jones (1990) also found *B. cederstroemi* along the southshore in 1987. We suspect that reduced alewife predation allowed the *B. cederstroemi* population to expand in 1987. In 1988, alewife abundance increased, but not to 1985–86 levels (Fig. 5). *Bythotrephes cederstroemi* did not occur in our zooplankton samples in 1988, but we did find it in abundance in alewife guts in April.

Nearshore Zooplankton Community

The zooplankton communities in the eastern basin and along the southern shore of Lake Ontario showed decreasing trends in zooplankton abundance between 1984 and 1987. At Nine Mile Point, zooplankton abundance in single samples collected in midsummer fell from $3 \times 10^6 \cdot m^{-2}$ (15 m depth: 0.7 km from shore) and $8 \times 10^6 \cdot m^{-2}$ (30 m: 1.6 km) in 1984 to between 500 and $1000 \cdot m^{-2}$ in 1987 and 1988 (Fig. 7). Changes in zooplankton abundance could not be examined at 50 m (2.9 km) and 100 m (6.8 km) because the 1984 and 1985 samples from those sites were not collected from the epilimnion. Decreased zooplankton abundances in 1987 and 1988 were also observed in the eastern basin (discussed earlier; Fig. 3) and along the southshore, 2 km off Oak Orchard and Smoky Point. Seasonal zooplankton abundances (average of monthly estimates), at the latter two sites, fell from $748 \times 10^3 \cdot m^{-2}$ in 1986 to $448 \times 10^3 \cdot m^{-2}$ in 1987. Decreased zooplankton abundance in 1987 and 1988 appears to be a widespread phenomenon covering the southshore and eastern basin. No samples were collected along the northshore. The extremely low abundance of *B. longirostris* at Nine Mile Point in 1987 also occurred at Oak Orchard, Smoky Point, and station 41 (midlake), suggesting that the reduced abundance of this species extended over much of the main lake. Although the average seasonal abundance of *B. longirostris* decreased in the eastern basin (station 81) from $320 \times 10^3 \cdot m^{-2}$ in 1986 to $222 \times 10^3 \cdot m^{-2}$ in 1987, the decrease was not as extreme as in the main lake where the population declined from $235 \times 10^3 \cdot m^{-2}$ in 1986 to $32 \times 10^3 \cdot m^{-2}$ in 1987.

The nearshore regions also showed similar shifts in cladoceran size structure towards smaller species. In the eastern basin the relative abundance of the larger clacoderan, *D. retrocurva*, decreased whereas the relative abundance of the smaller cladoceran, *B. longirostris*, increased (Fig. 8). On the southshore at Nine Mile Point, the dominant species of *Daphnia* switched during the 5 yr of the study (Fig. 9). In 1984, 1985, and 1988, *D. g. mendotae* was the only daphnid or co-dominant daphnid at Nine Mile Point. *Daphnia retrocurva* was dominant in 1986

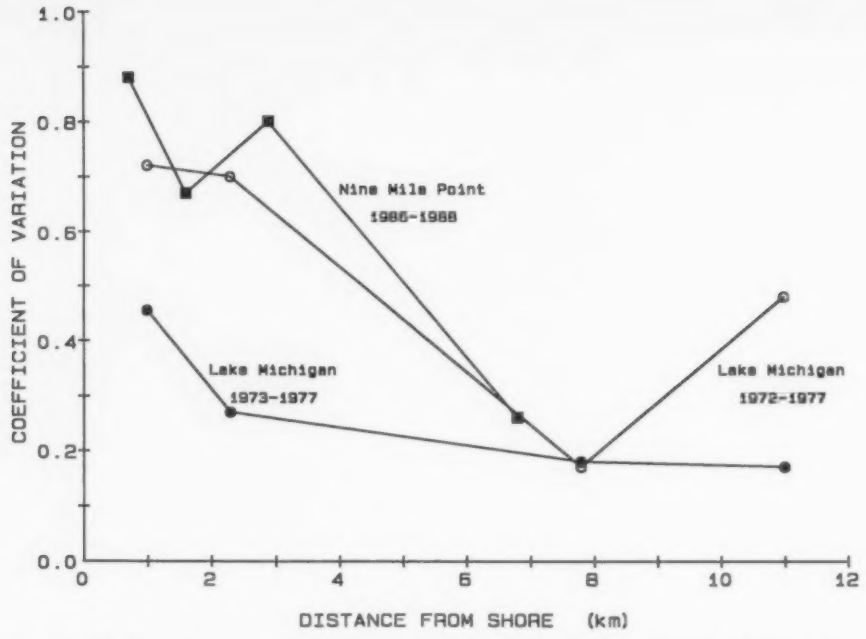


FIG. 12. Relationships between the coefficient of variation (standard deviation/mean) of the peak abundances of zooplankton in the July–August period, in three studies, and distance from shore. ○, Lake Michigan, 1972–77 (Evans et al. 1980); ●, Lake Michigan, 1973–77 (Evans et al. 1980. ■, Lake Ontario, Nine Mile Point, 1986–88. See text for derivation of data.

and 1987 and co-dominant in 1988. Changes in the *Daphnia* spp. complex can result from changes in size-selective predation (Brooks and Dodson 1965; Wells 1970; Evans and Jude 1986) or from sampling error. If one species of daphnid succeeded another during seasonal development, and if only one sample were collected each year, then a pattern of alternating dominance of species could result. Average temperatures prior to sampling (July 1–20) should correspond with annual rates of seasonal development of the zooplanktonn community. Temperature records were not available for Nine Mile Point but had been collected for the eastern basin. *Daphnia retrocurva* was dominant at Nine Mile Point in both the warmest (1987) and coldest (1986) years, suggesting that rate of seasonal development was not responsible for an apparent switching in daphnid dominance. Nor did we observe higher zooplankton abundance in the warmer years (1987 and 1988) as would be predicted from the relationship between the heat content of the water column and zooplankton abundance, derived for Lake Ontario by Patalas (1969). Differences in the rates of seasonal development do not account for the changes observed in the zooplankton community.

It is difficult to evaluate the cause(s) for the observed decrease in zooplankton abundance and changes in cladoceran composition with the data at hand. Decreases in zooplankton abundance can result from decreases in food supply (McQueen et al. 1986) and increases in predation pressure (Goad 1984; Evans 1986; McQueen et al. 1989). When zooplankton communities respond to increases in invertebrate predation, the species tend to be large (Lynch 1979). Vertebrate predation selects for smaller species and lower abundance (Brooks and Dodson 1965; Langeland 1982; McQueen et al. 1986). The shift in cladocerans towards smaller species and the decreases in zooplankton abundance during the 1984–88 period suggest that vertebrate predation increased from 1984 to 1987. However, the same changes could result from a combination of stable fish predation and reduced food supply, resulting possibly from the lower total phosphorus concentrations in the epilimnion in the summer (Stevens and Neilson 1987; Johannsson et al. 1991).

Nearshore–Offshore Gradients

Zooplankton seasonal development and epilimnetic abundance (number per square metre), density (number per cubic metre), and composition were examined along the nearshore–offshore gradients at Nine Mile Point, Smoky Point, and Oak Orchard. More rapid seasonal development in the nearshore was observed in June 1987 through factor analysis (Fig. 10) where development of the *B. longirostris* population paralleled the more rapid warming of the water column nearshore (Fig. 11). Earlier nearshore development of zooplankton populations, associated with earlier warming of the water column, has been reported previously for Lakes Ontario (Patalas 1969; Taylor et al. 1987) and Michigan (Evans et al. 1980). This spatial pattern can be modified by wind-induced water movements and river inputs (Czaika 1974, 1978; Simons and Schertzer 1987).

Annual variability in zooplankton abundance nearshore and offshore was examined by use of our Nine Mile Point data. For each depth, we calculated means, standard deviations, and coefficients of variation, but we omitted the 1984 and 1985 data because we sampled more deeply in those years than during 1986–88. The coefficient of variation of zooplankton abundance decreased with distance from shore (Fig. 12). This finding was corroborated by an examination of Evans et al.'s

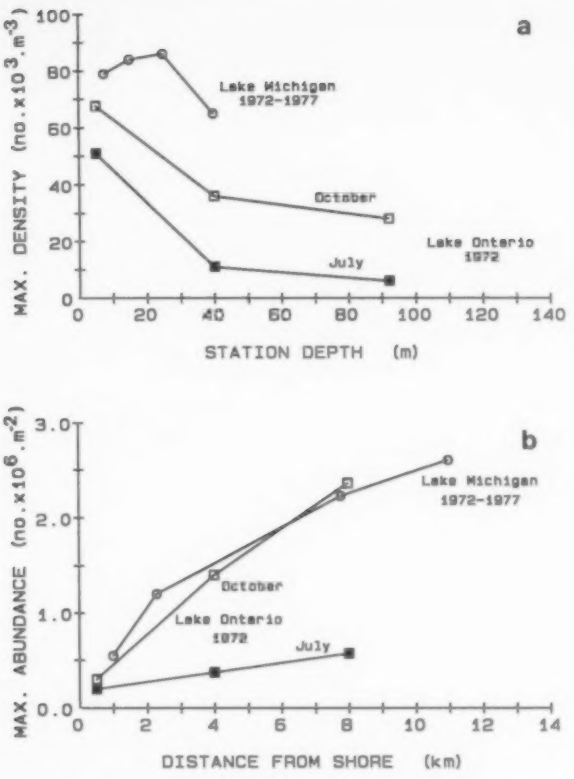


FIG. 13. Relationships between zooplankton density and station depth and between zooplankton abundance and distance from shore in samples collected from the whole water column. ○, Lake Michigan (Evans et al. 1980); ■, southshore of Lake Ontario, July–August (Czaika 1974); □, southshore of Lake Ontario, October, period of maximum abundance (Czaika 1974). See text for derivation of data and statistical analysis.

(1980) data from southeastern Lake Michigan (Fig. 12). The Lake Michigan zooplankton had been sampled monthly with a 153-μm-mesh net towed vertically to the surface from 2 m off the bottom. Evans et al. (1980) collected samples at 30 stations, divided amongst four depth ranges, from 1971 to 1977. For each depth range, we extrapolated the peak July or August zooplankton density for each year from fig. 2 of Evans et al. (1980), multiplied by the mean of the depth range, and calculated the means, standard deviations, and coefficients of variation. Because densities were extremely high in 1972 and contributed significantly to annual variability, the coefficient of variation was calculated including and excluding the 1972 data. Neither study provides information on the reason(s) for this relationship, but the greater number of biological interactions due to the larger number of species nearshore and the more disturbed physical regime nearshore may provide more scope for variation in this region.

Nearshore–offshore trends in zooplankton abundance (number per square metre) and density (number per cubic metre) in July–August were examined in epilimnetic and whole water column zooplankton samples: epilimnetic data came from Oak Orchard/Smoky Point and Nine Mile Point and whole water column data from Czaika (1974, Lake Ontario southshore 1972) (Fig. 13). Abundances in Czaika's (1974) study were calculated by multiplying the densities in her table 1 by the mean station depth (Czaika 1974, fig. 1). Two lines are presented in Fig. 13 because the summer of 1972 was very cold and zooplankton did not reach maximum abundances until October. Changes in zooplankton abundance and density with distance from shore were dependent on the type of sample collected. In whole water column samples, abundance of zooplankton increased offshore (Fig. 13b). The same trend was observed in the data from southeastern Michigan (Evans et al. 1980) (Fig. 13b). The sign test (Siegel 1956) was applied to the Lake Michigan data to test the significance of this relationship. Within each year's data, the direction of change in abundance between each pair of samples from adjacent depth strata was determined and tallied over the study period. Sixteen of 18 comparisons increased in the offshore sample ($p = 0.001$). As long as the abundance of zooplankton in the epilimnion does not decrease, abundance in the whole water column should increase offshore with the addition of metalimnetic and hypolimnetic organisms. Density of whole water column samples was highest in the nearshore and decreased by the 40-m depth contour (Fig. 13a). In epilimnetic zooplankton samples, no consistent relationship exists between abundance or density and distance from shore.

Factor analysis indicated that the nearshore and offshore zooplankton composition differed in summer (Fig. 10). The relative abundance of *B. longirostris* usually decreases with distance from shore, while that of *D. thomasi* usually increases (Table 2). The absolute abundance of *B. longirostris*, however, reaches its maximum between the 20- and 50-m depth contours, while that of *D. thomasi* continues to increase. Because the *D. thomasi* population is centred in the metalimnion (D. R. S. Lean, Hj. Frikker, and A. Abbott, National Water Research Institute, Department of the Environment, Burlington, Ont., unpubl. data), its population should increase offshore as more of the metalimnetic and hypolimnetic layers are included in the water column. Why *B. longirostris* is most abundant in the 20–50 m range is not known. The nearshore *Daphnia* complex is usually dominated by small species, such as *D. retrocurva* (Patalas 1969; McNaught and Buzzard 1973; Czaika 1974). This is also true in Lake Michigan (Evans and Jude 1986). Evans and Jude (1986) believed that this domination dates back at least until the early 1880's in Lake Michigan when large numbers of planktivorous fish inhabited the nearshore. As discussed above, in recent years we have also found *D. g. mendotae* in the nearshore in southeastern Lake Ontario.

Summary

The basic structure of the zooplankton community in Lake Ontario has not changed since the late 1960's. However, during the 1980's, abundance decreased both in the midlake and nearshore during the 1983–84 to 1987 period. In the nearshore, there was also a trend toward greater representation of smaller cladocerans in the community during the same period. In the midlake, no trend towards smaller species was observed, but FA of the less common, larger cladocerans occurred earlier in the season from 1985 to 1988 than from 1981 to 1984. CET and CPUE of alewife ⩾165 mm in U.S. waters in the spring were correlated with changes in FA. *Bythotrephes cederstroemi*, a recently introduced predatory cladoceran, was found only in 1987. Its presence may have been associated with reduced alewife CPUE that year.

TABLE 2. Relative abundances (RA, % of total zooplankton abundance) and absolute abundances (AA, $no \cdot m^{-2}$) of *B. longirostris* and *D. thomasi* at different distances from shore in Lakes Ontario and Michigan in July of various years.

Location	Year(s)	Bottom depth (m)	Distance from shore (km)	*B. longirostris* RA (%)	*B. longirostris* AA ($no \cdot m^{-2}$)	*D. thomasi* RA (%)	*D. thomasi* AA ($no \cdot m^{-2}$)
Lake Ontario, southshore (Czaika 1974)	1972	5–6	0.5	62	163	0	1
		13–60	4.0	45	199	2	10
		75–129	8.0	21	122	8	48
Lake Ontario, Oak Orchard and Smoky Point	1986	25	2.0	51	820	36	613
		190	20.0	23	450	57	1158
	1987	25	2.0	—	—	21	206
		190	20.0	—	—	49	207
Lake Ontario, Nine Mile Point	1986	15	1.0	65	1240	25	468
		30	1.7	78	1018	18	238
		50	2.7	76	1566	16	328
		100	6.3	43	513	45	531
	1987	15	1.0	—	—	26	134
		30	1.7	—	—	14	37
		50	2.7	—	—	15	43
		100	6.3	—	—	31	342
	1988	15	1.0	70	283	18	73
		30	1.7	52	546	23	244
		50	2.7	48	467	24	235
		100	6.3	40	281	33	230
Lake Michigan (Evans et al. 1980)	1973–77	5–10	1.0	53	165	1	2
		10–20	2.0	47	364	2	18
		20–30	5.0	38	869	6	120
		30–50	11.6	26	472	7	127

Trends in zooplankton composition, density, abundance, and seasonal development along the nearshore–offshore gradient in Lake Ontario were corroborated by those in Michigan (1974–77), when it also was an alewife-dominated system. Seasonal development occurred earlier in the nearshore. Interannual variability in abundance was greater in the nearshore. In whole water column samples, maximum zooplankton density occurred in the nearshore, while abundance decreased offshore. In epilimnetic samples, neither abundance nor density was affected by distance from shore. The relative abundance of *B. longirostris* was greatest inshore, with the maximum absolute abundance occurring between the 20- and 50-m depth contours. *Diacyclops thomasi* reached maximum absolute and relative abundances offshore. The nearshore *Daphnia* complex was generally dominated by small species, such as *D. retrocurva*.

Acknowledgements

We wish to thank Dr. J. McLaren for making available the Somerset Monitoring Report of the New York State Electric and Gas Corporation. We would also like to thank Mr. C. Schneider and the crews of the R/V's *Kaho* and *Seth Green* for sampling zooplankton and alewife in US waters and the captains and crews of the C.C.S. *Bayfield* who collected the midlake (station 41) and eastern basin (station 81) samples. The following people have contributed to the paper through discussion or review of the manuscript, and we thank them for their time and ideas: Dr. J. Gannon, Dr. U. Borgmann, Mr. J. Moore, and several referees.

References

BEETON, A. M. 1960. The vertical migration of *Mysis relicta* in Lakes Huron and Michigan. J. Fish. Res. Board Can. 17: 517–540.

BROOKS, J. L., AND S. I. DODSON. 1965. Predation, body size and composition of plankton. Science (Wash., DC) 150: 28–35.

BUTORINA, L. G., AND I. I. SOROKIN. 1966. Food of *Polyphemus pediculus* (L.). Plankton i Bentos Vnutr. Vod. 12: 170–174. (In Russian cited in Champ and Pourriot 19770

CARPENTER, G. F., E. L. MANSEY, AND N. H. F. WATSON. 1974. Abundance and life history of *Mysis relicta* in the St. Lawrence Great Lakes. J. Fish. Res. Board Can. 31: 319–325.

CHAMP, P., AND R. POURRIOT. 1977. L'alimentations des cladoceres planctoniques dulcaquicoles. Ann. Biol. 16: 317–342.

COOLEY, J. M., J. E. MOORE, AND W. T. GEILING. 1986. Population dynamics, biomass, and production of the macrozooplankton in the Bay of Quinte during changes in phosphorus loadings, p. 166–176. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

CZAIKA, S. C. 1974. Crustacean zooplankton of southwestern Lake Ontario in 1972 during the International Field Year for the Great Lakes. International Association of Great Lakes Research. Proc. Conf. Great Lakes Res. 17: 1–16.

1978. Crustacean zooplankton of southwestern Lake Ontario in spring 1973 and at the Niagara and Genesee River mouth areas in 1972 and spring 1973. J. Great Lakes Res. 4: 1–9.

EVANS, M. S. 1986. R ecent major declines in zooplankton populations in the inshore region of Lake Michigan: probable causes and implications. Can. J. Fish. Aquat. Sci. 43: 154–159.

EVANS, M. S., B. E. HAWKINS, AND D. W. SELL. 1980. Seasonal features of zooplankton assemblages in the nearshore area of southeastern Lake Michigan. J. Great Lakes Res. 6: 275–289.

EVANS, M. S., AND D. J. JUDE. 1986. Recent shifts in *Daphnia* community structure in southeastern Lake Michigan: a comparison of the inshore and offshore regions. Limnol. Oceanogr. 31: 56–67.

GAUCH, H. G. JR. 1982. Multivariate analysis in community ecology. Cambridge University Press, Cambridge, UK. 298 p.

GOAD, J. A. 1984. A biomanipulation experiment in Green Lake, Seattle, Washington. Arch. Hydrobiol. 102: 137–153.

GROSSNICKLE, N. E. 1982. Feeding habits of *Mysis relicta* — an overview. Hydrobiologia 93: 101–107.

HANEY, J. G., AND D. J. HALL. 1973. Sugar-coated *Daphnia*: preservation technique for Cladocera. Limnol. Oceanogr. 18: 331–333.

INTERNATIONAL JOINT COMMISSION. 1989. Report on Great Lakes water quality. Report of the Great Lakes Water Quality Board, International Joint Commission, 100 Ouellette Ave., Suite 800, Windsor, Ont. N9A 6T3. 128 p.

JOHANNSSON, O. E. 1987. Comparison of Lake Ontario zooplankton communities between 1967 and 1985: before and after implementation of salmonid stocking and phosphorus control. J. Great Lakes Res. 13: 328–339.

JOHANNSSON, O. E., AND C. K. MINNS. 1987. Examination of association indices and formulation of a composite seasonal dissimilarity index. Hydrobiologia 150: 109–121.

JOHANNSSON, O. E., AND R. O'GORMAN. 1991. The roles of predation, food, and temperature in structuring the epilimnetic zooplankton populations in Lake Ontario, 1981–1986. Trans. Am. Fish. Soc. 120: 193–208.

JOHANNSSON, O. E., K. M. RALPH, R. DERMOTT, M. A. NEILSON, AND E. S. MILLARD. 1991. Trends in nutrient and biological variables in the offshore: a preliminary report of the Lake Ontario Biomonitoring Program. Lake Ontario Fisheries Unit 1990 Annual Report. Chap. 12.

LANGE, C., AND R. CAP. 1986. *Bythotrephes cederstroemi* (Schodler) (Cercopagidae: Cladocera): a new record for Lake Ontario. J. Great Lakes Res. 12: 142–143.

LANGELAND, A. 1982. Interactions between zooplankton and fish in a fertilized lake. Holarct. Ecol. 5: 273–310.

LYNCH, M. 1979. The evolution of cladoceran life histories. Q. Rev. Biol. 55: 23–42.

MAKAREWICZ, J. C., AND D. JONES. 1990. The establishment of *Bythotrephes cederstroemi* in the offshore of Lake Ontario. J. Great Lakes Res. 16: 143–147.

MCNAUGHT, D. C., AND M. BUZZARD. 1973. Changes in zooplankton populations in Lake Ontario (1939–1972). International Association of Great lakes Research. Proc. Conf. Great Lakes Res. 16: 76–86.

MCQUEEN, D. J., M. R. JOHANNES, J. R. POST, T. J. STEWART, AND D. R. S. LEAN. 1989. Bottom-up and top-down impacts on freshwater pelagic community structure. Ecol. Monogr. 59: 289–309.

MCQUEEN, D. J., AND J. R. POST. 1988. Limnocorral studies of cascading trophic interactions. Verh. Int. Ver. Limnol. 23: 739–747.

MCQUEEN, D. J., J. R. POST, AND E. L. MILLS. 1986. Trophic relationships in freshwater pelagic ecosystems. Can. J. Fish. Aquat. Sci. 43: 1571–1581.

MILLS, E. L., AND J. L. CONFER. 1986. Computer processing of zooplankton – application in fisheries studies. Fisheries (Bethesda) 11: 24–27.

MILLS, E. L., D. M. GREEN, AND A. SCHIAVONE. 1987. Use of zooplankton size to assess the community structure of fish populations in freshwater lakes. N. Am. J. Fish. Manage. 7: 369–378.

MILLS, E. L., AND A. SCHIAVONE JR. 1982. Evaluation of fish communities through assessment of zooplankton populations and measures of lake productivity. N. Am. J. Fish. Manage. 2: 14–17.

NEILSON, M. A., AND R. R. J. STEVENS. 1987. Spatial heterogeneity of nutrients and organic matter in Lake Ontario. Can. J. Fish. Aquat. Sci. 44: 2192–2203.

NILSSON, N. A. 1979. Food and habitat of the fish community of the offshore region of Lake Vanern, Sweden. Inst. Freshwater Res. Drottningholm Rep. 58: 126–139.

O'GORMAN, R., D. H. BARWICK, AND C. A. BOWEN. 1987a. Discrepancies between ages determined from scales and otoliths for alewives from the Great Lakes, p. 203–210. *In* R. C. Summerfelt and G. E. Hall [ed.] Age and growth of fish. Iowa State University Press, Ames, IA.

O'GORMAN, R., R. A. BERGSTEDT, AND T. H. ECKERT. 1987b. Prey fish dynamics and salmonine predator growth in Lake Ontario, 1978–84. Can. J. Fish. Aquat. Sci. 44: 390–403.

O'GORMAN, R., AND C. P. SCHNEIDER. 1986. Dynamics of alewives in Lake Ontario following a mass mortality. Trans. Am. Fish. Soc. 115: 1–14.

OLSON, R. A., J. D. WINTER, D. C. NETTLES, AND J. M. HAYNES. 1988. Resource partitioning in summer by salmonids in south-central Lake Ontario. Trans. Am. Fish. Soc. 117: 552–559.

PATALAS, K. 1969. Composition and horizontal distribution of crustacean plankton in Lake Ontario. J. Fish. Res. Board Can. 26: 2135–2164.

1972. Crustacean zooplankton and the eutrophication of St. Lawrence Great Lakes. J. Fish. Res. Board Can. 29: 1451–1462.

POST, J. R., AND D. J. MCQUEEN. 1987. The impact of planktivorous fish on the structure of a plankton community. Freshwater Biol. 17: 79–90.

SIEGEL, S. 1956. Nonparametric stastistics for the behaviourial sciences. McGraw-Hill Book Company, Inc., Toronto, Ont. 312 p.

SIMONS, T. J., AND W. M. SCHERTZER. 1987. Stratification, currents, and upwelling in Lake Ontario, summer 1982. Can. J. Fish. Aquat. Sci. 44: 2047–2058.

SPRULES, W. G., H. P. RIESSEN, AND E. H. JIN. 1990. Dynamics of the *Bythotrephes* invasion of the St. Lawrence Great Lakes. J. Great Lakes Res. 16: 346–351.

STEVENS, R. J. J., AND M. A. NEILSON. 1987. Response of Lake Ontario to reductions in phosphorus load, 1967–82. Can. J. Fish. Aquat. Sci. 44: 2059–2068.

TAYLOR, W. D., H. J. FRICKER, AND D. R. S. LEAN. 1987. Zooplankton seasonal succession in Lake Ontario at northshore, midlake, and southshore stations in 1982, and a comparison with 1970. Can. J. Fish. Aquat. Sci. 44: 2178–2184.

WATSON, N. H. F., AND G. F. CARPENTER. 1974. Seasonal abundance of crustacean zooplankton and net plankton biomass of Lakes Huron, Erie, and Ontario. Can. J. Fish. Aquat. Sci. 31: 309–317.

WELLS, L. 1968. Seasonal depth distribution of fish in southeastern Lake Michigan. Fish. Bull. 67: 1–15.

1970. Effects of alewife predation on zooplankton populations in Lake Michigan. Limnol. Oceanogr. 15: 556–565.

WILKINSON, L. 1988. SYSTAT: the system for statistics. SYSTAT, Inc., Evanston, IL. 821 p.

WILSON, J. B., AND J. C. ROFF. 1973. Seasonal vertical distributions and diurnal migration patterns of Lake Ontario crustacean zooplankton. International Association for Great Lakes Research. Proc. Conf. Great Lakes Res. 16: 190–203.

Status and Trends of the Lake Ontario Macrobenthos[1]

Thomas F. Nalepa

Great Lakes Environmental Research Laboratory, 2205 Commonwealth Blvd., Ann Arbor, MI 48105, USA

Nalepa, T. F. 1991. Status and trends of the Lake Ontario macrobenthos. Can. J. Fish. Aquat. Sci. 48: 1558–1567.

The benthic macroinvertebrate community of Lake Ontario was examined relative to communities found in the other Great Lakes and also relative to trends over time. In the nearshore, populations are heavily influenced by municipal and industrial inputs. For example, oligochaete abundances in the nearshore are higher than in any of the other Great Lakes (excluding shallow Lake Erie), communities have been altered even to relatively deep depths near the major river mouths, and the pollution-sensitive *Pontoporeia hoyi* is scarce along the southern shoreline east of the Niagara River mouth. In the profundal, benthic composition is similar to that found in the other Great Lakes, but biomass is less than might be expected given the amount of organic material settling to the bottom. Benthic standing stocks in this region have apparently declined almost threefold since the 1960s. Reasons for this decline do not appear to be related to trends in water column productivity or to predation pressure, but may be related to the accumulation of contaminants. Research needs include studies to assess benthic trends over a much broader area of the lake and studies to examine the impact of sublethal levels of contaminants.

La communauté des macroinvertébrés benthiques du lac Ontario a été comparée à d'autres communautés des Grands Lacs et son évolution a été examinée. Près des rives, les populations animales sont gravement affectées par les déchets municipaux et industriels. Par exemple, les oligochètes sont plus abondants dans le lac Ontario que dans tous les autres Grands Lacs (sauf le lac Érié, lequel est peu profond) près des rives; les communautés ont subi des changements même dans les eaux relativement profondes près de l'embouchure des principales rivières et; *Pontoporeia hoyi*, organisme sensible à la pollution, est rare le long de la rive sud à l'est le l'embouchure de la rivière Niagara. Dans les profondeurs, la composition du benthos est semblable à celle des autres Grands Lacs, mais la biomasse est inférieure à ce qu'on pourrait s'attendre vu la quantité importante de matière organique déposant au fond. Les stocks d'organismes benthiques de cette région sont apparemment presque trois fois moins importants que dans les années 1960. Il ne semble pas que ce déclin soit attribuable à une chute de la productivité biologique du lac ou à une prédation accrue : il serait plutôt relié à l'accumulation des contaminants. Les recherches futures devront tenter d'évaluer l'évolution du benthos en couvrant une portion du lac beaucoup plus importante et, par ailleurs, examiner l'impact de doses subléthales de contaminants.

Received January 24, 1989
Accepted June 26, 1990
(JA032)

Reçu le 24 janvier 1989
Accepté le 26 juin 1990

As a result of numerous field investigations over the past few decades, our knowledge of the benthic community in Lake Ontario is perhaps the most extensive of any of the Great Lakes. Surveys over the entire lake (Hiltunen 1969; Kinney 1972; Nalepa and Thomas 1976; Golini 1979) and more limited surveys in the open waters and in selected bays, harbors, and nearshore areas (Judd and Bocsor 1972; Brinkhurst 1970; Johnson and Matheson 1968; Johnson and Brinkhurst 1971; Barton and Hynes 1978; Johannsson et al. 1985a; Johnson and McNeil 1986; Barton 1986) have not only provided information on abundance and composition, but have also provided insights into some of the more important factors which influence distributions. In addition, the major findings of these surveys have been summarized in two excellent review articles. One review gave a historical perspective of benthic research throughout the Great Lakes, examined the taxonomic status of Great Lakes fauna, and provided a zoogeographical perspective of distributional patterns (Cook and Johnson 1974). More specifically, benthic communities in Lake Ontario were described and compared with communities found in the other Great Lakes. A more detailed, systematic review of the Lake Ontario benthos was presented in a summary of findings up until about 1976 (Mozley 1990). Distributions and relative abundances were given for each common species, along with pertinent information on life cycle, habitat, and feeding modes. Also, spatial distribution patterns were described and related to such factors as water depth, water quality, and physicochemical features of the sediments.

This review is not intended to be an exhaustive account of the Lake Ontario benthos, since, as noted above, detailed summaries have already been presented. Rather, its purpose is to focus on features of the benthos that are unique to this lake when compared with the other Great Lakes and to examine long-term trends in populations. Since most benthic studies in Lake Ontario have examined only the macrobenthos, or those invertebrates retained on a screen with 0.5- to 0.6-mm mesh openings, this review will be limited to this group of organisms.

Distinctive and Comparative Features of the Lake Ontario Benthos

Nearshore

Because species composition and distributions in relation to depth and substrate are generally similar to those found in the other Great Lakes (Cook and Johnson 1974), most distinctive

[1]GLERL Contribution No. 654.

TABLE 1. Total mean abundance of macroinvertebrates (thousands per square metre) at different depth intervals in each of the Great Lakes except Lake Erie. The data are taken from surveys conducted in the 1960s and early 1970s. Each survey employed similar sampling and sorting techniques.

Lake	Year sampled	Depth interval (m) 14–30	31–50	51–90	>90
Superior	1970[a]	0.2	1.0	0.9	0.3
Huron	1970[a]	2.9	3.4	3.0	
Michigan	1964–67[b]	6.2	10.5	5.9	2.9
Ontario	1964[c]	14.7	15.2		2.3
	1972[d]	8.8	7.2	8.1	1.2

[a]Schelske and Roth (1973).
[b]Alley and Mozley (1975).
[c]Hiltunen (1969).
[d]Nalepa and Thomas (1976).

features of nearshore benthic populations in Lake Ontario can be attributed to the great impact of polluting substances. Of the Great Lakes, Lake Ontario receives the largest burden of municipal and industrial effluents, mainly via the Niagara River (Allan et al. 1983). Excluding atypically shallow Lake Erie, total mean abundance of the benthos in Lake Ontario's nearshore region (<30 m), at least in the 1960s and early 1970s, was higher than abundances in nearshore regions of the other three Great Lakes (Table 1). These relatively high abundances, along with dominance of the community by oligochaetes (72% of the total; Nalepa and Thomas 1976), are a general reflection of the enriched nature of the nearshore zone. Nutrients enter this zone from the major rivers and concentrations tend to remain high because of the prominent thermal bar in the spring, which traps nutrients along the shoreline and stimulates phytoplankton productivity (Shiomi and Chawla 1970), and also because of the frequency of upwelling episodes later in the year, which replenishes depleted nutrient supplies (Stadelmann and Fraser 1974).

In most of the other Great Lakes, the impact of pollution on the benthic community is mainly restricted to nearshore areas, harbors, river mouths, and the shallow bays and basins. However, because of Lake Ontario's relatively small surface area and steep contours, an impacted fauna is evident even at relatively great depths off the major river mouths. For example, the amphipod *Pontoporeia hoyi* and the oligochaete *Stylodrilus herigianus*, both oligotrophic indicator species, were found in reduced numbers at depths as great as 70 m directly off the mouth of the Niagara River (Kinney 1972). Also, reduced numbers of the same two species, along with high densities ($46\,000 \cdot m^{-2}$) of the pollution-tolerant oligochaete *Tubifex tubifex*, were found at a depth of 54 m off Toronto Harbour (Nalepa and Thomas 1976). These distributions demonstrate the widespread and profound impact of riverborne pollutants on the Lake Ontario benthos. Not coincidently, some of the highest oligochaete densities ever reported from the Great Lakes have been from Lake Ontario or surrounding harbors. For example, densities of $61\,700 \cdot m^{-2}$ have been found near the mouth of the Niagara River (Nalepa and Thomas 1976) and up to $200\,000 \cdot m^{-2}$ have been reported from Toronto Harbour (Brinkhurst 1970).

Considering its habitat preferences and distribution patterns in the other Great Lakes, in no other open water area of the Great Lakes is there such a widespread scarcity of *Pontoporeia hoyi* as along the southern shoreline of Lake Ontario. Low densities in the area east of the Niagara mouth to Rochester at depths up to 30 m have been attributed to the deposition of riverborne pollutants (Hiltunen 1969; Nalepa and Thomas 1976). An alternative explanation for the scarcity of *Pontoporeia* in this area, however, is completely unrelated to loadings from the Niagara River. The prevailing westerly winds tend to pile up water along the southern shoreline, causing the downwelling of warm, epilimnetic waters (to 19°C) (Lee 1972). *Pontoporeia*, a glaciomarine relict, does best when temperatures are consistently less than 10°C (Smith 1972), and populations may be adversely affected by these frequent intrusions of warmer water. Another possible theory for the lack of *Pontoporeia* along the southern shoreline may be derived from examining the distribution of *Stylodrilus*. Like *Pontoporeia*, *Stylodrilus* is a pollution-sensitive form and also a coldwater stenotherm (Mozley and Howmiller 1977). Yet, although not found directly off the Niagara River mouth, it was found in great numbers in the same areas where *Pontoporeia* was absent (Nalepa and Thomas 1976). In laboratory bioassays, *Stylodrilus* was found to be relatively sensitive (compared with other oligochaete species) to high temperatures and conditions associated with organic pollution (i.e. sewage sludge, anoxia) (Chapman et al. 1982a, 1982b). This finding was not unexpected considering its distribution in the field. However, it was also found to be relatively more tolerant of certain chemical compounds that might otherwise be considered toxic. Because *Stylodrilus* occurs in great numbers along the southern shoreline, the low densities of *Pontoporeia* in this area may not be from the relatively higher water temperatures or from organic loadings from the Niagara River, but from chemical contaminants that may be affecting this organism specifically. The Niagara River is the source of many persistent contaminants, and high levels of mirex, PCBs, and mercury among other chemicals have been noted along the southern shoreline (Thomas 1983). Unfortunately, despite its importance in Lake Ontario and the rest of the Great Lakes, the relative tolerance of *Pontoporeia* to various types of chemical pollutants has not been thoroughly investigated. In laboratory experiments, this species avoided sediments from polluted harbors (Gannon and Beeton 1969), but its response to specific contaminants remains largely unknown.

Another noteworthy aspect of benthic distributions in nearshore Lake Ontario is the scarcity of insect fauna along the northern shoreline; the number and diversity of both mayflies and trichopterans in the wave zone (0–2 m) were impoverished compared with the fauna in similar areas in Lakes Superior, Huron, and Erie (Barton and Hynes 1978). It was hypothesized that the frequent upwelling of cold, hypolimnetic water in the summer may limit populations either by killing them directly or by preventing the number of degree-days needed for complete life-cycle development. Another factor mentioned as being potentially harmful was the poor water quality of the nearshore zone. In comparing nearshore (5–20 m) benthic communities of Lakes Ontario and Huron, Barton (1986) noted fewer species but greater abundances in Lake Ontaro in all types of substratum; this suggests more enriched conditions in Lake Ontario.

Offshore

While the benthic community of nearshore Lake Ontario is variable and dependent upon proximity to waste inputs, the community found in offshore areas is more uniform and con-

TABLE 2. Comparison of water column productivity, organic sedimentation rates, and benthic biomass in the profundal (>90 m) in Lakes Superior (Whitefish Bay), Michigan, and Ontario. Dry-weight biomass was converted to organic carbon by assuming an organic carbon content of 50%. The sedimentation rate for Lake Superior was for the July–September period, while the sedimentation rate for the other two lakes was for the April–November period.

Variable	Lake		
	Superior	Michigan	Ontario
Chlorophyll *a* ($mg \cdot m^{-2}$)		20–80[a]	60–120[b]
Primary production ($g\ C \cdot m^{-2} \cdot y^{-1}$)		100–140[c]	170–220[d]
Sedimentation rate ($mg\ C \cdot m^{-2} \cdot d^{-1}$)	46[e]	104[f]	176[g]
Sediment carbon content (%)	1–3[h]	3–5[i]	3–4[j]
Benthic biomass ($g\ C \cdot m^{-2}$)	1.1[k]	0.9[l]	0.4[m]
Biomass composition (%)			
Pontoporeia hoyi	91	69	85
Oligochaeta	8	26	14

[a]Parker et al. (1977) and Bartone and Schelske (1982).
[b]Charlton (1983).
[b]Parker et al. (1977) and Fee (1973).
[d]Stadelmann et al. (1974).
[e]Eadie (Great Lakes Environmental Research Laboratory, Ann Arbor, MI, unpublished data).
[f]Eadie et al. (1984).
[g]Rosa (1985).
[h]Thomas and Dell (1978).
[i]Cahill (1981).
[j]Thomas et al. (1972) and Nalepa and Thomas (1976).
[k]Nalepa et al. (1988).
[l]Nalepa (1989).
[m]Johannsson et al. (1985a).

sistent. Like offshore communities in the other Great Lakes, the dominant form is *Pontoporeia* followed by oligochaetes, of which most are *Stylodrilus* (Cook and Johnson 1974). Yet, although similar in composition, standing stocks of the macrobenthos in the profundal (>100 m) are lower than might be expected given the productivity of the system. In Table 2, benthic biomass and composition, organic inputs, and water column productivity in the profundal of Lake Ontario are shown relative to most of the same variables in two other profundal regions of the Great Lakes. Inputs were determined from amounts of organic carbon collected in sedimentation traps placed just below the thermocline. In most lake systems, standing stocks of the macrobenthos are generally related to variables indicative of water column productivity, i.e. chlorophyll *a*, total phosphorus, and Secchi disc transparency (Hanson and Peters 1984; Rasmussen and Kalff 1987). Organic material produced in the water column eventually settles to the bottom and serves as food for the benthos. While the amount of organic carbon settling from the epilimnion in Lake Ontario was far greater than in Lake Michigan or in Lake Superior (Whitefish Bay), benthic biomass was less than one half the biomass found in these other two lakes (Table 2). In all three profundal areas, *Pontoporeia* was the dominant form, accounting for 69–91% of the biomass total.

Persistent Contaminants

Because of the high contaminant loads into Lake Ontario, benthic organisms in both nearshore and offshore areas are exposed to elevated levels of many persistent chemicals. Yet, the impacts of acute and chronic exposures are not readily discernible from the many other environmental factors that can influence benthic abundances and distributions (Nalepa and Landrum 1988). Only one study in Lake Ontario has clearly shown a negative relationship between a specific chemical compound and benthic abundances. In Hamilton Bay, oligochaetes (and all other organisms) were absent from an area having an iron content greater than 25% (Johnson and Matheson 1968). Even at these high concentrations, however, the conclusion was that the iron content per se was not necessarily detrimental, but conditions associated with the high iron levels, such as high oxygen demand and continuous inorganic siltation, were likely responsible for the observed effect. While several studies in nearshore areas have implicated heavy metals in having a negative impact on the nearshore benthic community (Hart et al. 1986; Poulton et al. 1988), other factors including organic pollution were also recognized as an influencing factor.

TABLE 3. Mean concentration of various contaminants in the sediments of depositional zones in four of the Great Lakes.

Lake	Contaminant (ppb)			Source
	PCB	HEOD	DDT	
Superior	4.8	0.25		Frank et al. 1980
Huron	15.0	<0.20	18.4	Frank et al. 1979b
Michigan	17.3	0.41	24.4	Frank et al. 1981
Ontario	85.0	0.50	62.2	Frank et al. 1979a

On a lakewide basis, benthic populations are probably most influenced by low, sublethal levels of contaminants because low concentrations of contaminants are more widespread and occur throughout the offshore depositional basins of the lake. Contaminant levels in the depositional basins of Lake Ontario are higher than levels in the depositional basins of the other Great Lakes (Table 3). Although no studies of Lake Ontario sediments or benthos have been specifically designed to assess the effects of low-level, long-term exposures, some evidence suggests that such effects may exist. In laboratory experiments, sublethal effects were apparent at lower concentrations than those reported from Lake Ontario sediments. For instance, *Stylodrilus* ceased feeding after 58 d at PCB concentrations over $50\ ng \cdot g^{-1}$ (D. S. White, Murray State University, Murray, KY, unpublished data). Concentrations this high are found over broad areas in Lake Ontario, with concentrations greater than $200\ ng \cdot g^{-1}$ quite common (Thomas 1983). Similarly, while zinc concentrations of between 58.5 and 123.5 $\mu g \cdot g^{-1}$ lowered the swimming activity of *Pontoporeia* (Magnuson et al. 1976), concentrations of 100–500 $\mu g \cdot g^{-1}$ have been reported from the surficial sediments of Lake Ontario (Mudroch 1983). In a study on the effects of long-term exposures to the chlorinated pesticide endrin, reworking rates of *Stylodrilus* were affected by concentrations as low as $3.1\ ng \cdot g^{-1}$ (Keilty et al. 1988b); endrin concentrations in sediments from some nearshore sites in Lake Ontario were as high as $29\ ng \cdot g^{-1}$ (Stevens 1987). While results of laboratory experiments may not be applicable to the field situation, these studies do demonstrate the potential for long-term chronic impacts on populations.

Consistent with higher contaminant levels in the sediments, levels in the benthos also appear to be higher in Lake Ontario when compared with other parts of the Great Lakes system (Table 4). In addition, bioaccumulation factors (BAF, i.e. concentration in organism/concentration in sediments) indicate a significant increase in organism levels over sediment levels. For instance, oligochaetes had a BAF of 2–8, while *Pontopor-*

TABLE 4. Levels of various contaminants found in benthic macroinvertebrates in the Great Lakes. The number in parentheses is the bioaccumulation factor (concentration in organism/concentration in sediment) (modified from Nalepa and Landrum 1988).

Organism	Organic contaminant (ng·g·dry wt^{-1}) PCB	DDE	DDD	HEOD	HCB	Location	Source
Pontoporeia	4215–11 000 (9.0–19.0)				230–895 (1.6–6.0)	4 sites, western Lake Ontario	Fox et al. 1983
Pontoporeia	1378	292		226		3 sites, western Lake Ontario	Whittle and Fitzsimons 1983
Pontoporeia	1849	730		376		1 site, eastern Lake Ontario	Whittle and Fitzsimons 1983
Pontoporeia	560	58	62	35		1 site, eastern Lake Erie	Whittle and Fitzsimons 1983
Pontoporeia	1305	154	96	141		1 site, eastern Lake Michigan	Evans et al. 1982
Oligochaeta	930–3650 (2.4–7.8)				105–735 (0.7–2.3)	4 sites, western Lake Ontario	Fox et al. 1983
Oligochaeta	440 (0.7)	5.9 (4.9)	1.5 (0.7)		3.6 (1.2)	1 site, Detroit River	Smith et al. 1985

TABLE 5. Benthic surveys conducted in the open waters of Lake Ontario.

Study	Year	Stations	Sampler	Mesh
Adamstone 1924	1922	7	Ekman	"Factory cotton"
Hiltunen 1969	1964	24	Smith–McIntyre	595 μm
Kinney 1972	1967–69	38	Ponar	595 μm
Nalepa and Thomas 1976	1972	55	Ponar	595 μm
Golini 1979	1977	153	Shipek	153 μm
Johannsson et al. 1985a	1981–83	4	Ponar	250 μm

eia had a BAF of 9–19 for PCBs in western Lake Ontario (Fox et al. 1983). These bioaccumulation factors are, of course, important when considering the transfer of contaminants to higher trophic levels. Of particular importance is the body burden and BAF of *Pontoporeia*, since it is an effective bioaccumulator of organic contaminants (Landrum 1988) and also a preferred food item of many Great Lakes fish (Mozley and Howmiller 1977). When PCB concentrations in various sized organisms in Lake Ontario were compared, *Pontoporeia*, slimy sculpin (*Cottus cognatus*), and lake trout (*Salvelinus namaycush*) had higher PCB concentrations than might be expected from a strict size-dependent relationship (Borgmann and Whittle 1983). Lake trout feed on slimy sculpin, which, in turn, feed on *Pontoporeia*.

Long-Term Trends

The open waters of Lake Ontario were first sampled quantitatively in 1922 when Adamstone (1924) gave abundances of the major benthic groups in seven samples taken on a transect from Toronto to the mouth of the Niagara River. Unfortunately, further openwater surveys were not conducted until four decades later. Then, within a 14-yr period (1964–77), five lake-wide surveys were conducted (Table 5) along with numerous localized surveys in bays, harbors, and adjacent waters. This period of intense sampling in the late 1960s and early 1970s was prompted by the demonstrated usefulness of benthic communities as indicators of trends in environmental quality. The Great Lakes were becoming increasingly eutrophic, and trends in benthic populations provided a basis for assessing the severity of the problem. Studies to assess changes in the benthic community in many portions of the Great Lakes indicated a degradation of environmental quality in the 1960s compared with a period some 10–30 yr earlier (Carr and Hiltunen 1965; Robertson and Alley 1966; Schneider et al. 1969; Howmiller and Beeton 1971). Unfortunately, in Lake Ontario, long-term trends in benthic populations during this period could not be established simply because good quantitative data were not available prior to the 1960s. As noted, the only quantitative, open-lake data available for Lake Ontario prior to the 1960s were from the survey of Adamstone (1924), and his sampling techniques probably underestimated the benthos when compared with the more quantitative techniques used in later surveys.

Since most surveys in the 1960s and thereafter employed similar techniques, comparisons at selected sites should provide an indication of any recent changes in benthic populations. The first comparison involves abundances reported in 1964 (Hiltunen 1969) and in 1972 (Nalepa and Thomas 1976). Stations of these two surveys that were of similar depth and location were paired and then compared (total of 13 pairs). Abundances of all groups were lower in 1972 than in 1964, particularly at the deeper stations (>100 m), and the difference was significant (sign test; $P<0.05$) over all 13 locations for sphaeriids and chironomids (Table 6). Total mean abundance of the benthos was 10 200·m^{-2} in 1964 compared with only 5400·m^{-2} in 1972. In terms of species composition, the oligotrophic indicator *Stylodrilus* accounted for a greater percentage of the oligochaete community in 1972 when compared with 1964, but this increase was not significant (sign test; $P<0.05$). On the other hand, the chironomid *Heterotrissocladius*, also an oligotrophic indicator, accounted for a significantly (sign test; $P<0.05$) lower percentage of the chironomid community in 1972. Although different grabs were used in the two surveys (Table 5), potential differences resulting from the sampling device appear to be irrelevant. Hiltunen used a Smith–McIntyre for collection, while Nalepa and Thomas used a Ponar; the latter grab is at least as efficient as the former and, in fact, consistently collected more sphaeriids in comparative trials (Powers and Robertson 1967). Seasonal influences would be minimal, since both surveys were conducted in the fall. To further examine the apparent decline in numbers between 1964 and 1972,

TABLE 6. Comparison between abundances (thousands per square metre) of major benthic taxa found in 1964 (Hiltunen 1969) and 1972 (Nalepa and Thomas 1976) at each of 13 different locations.

Station number		Depth (m)		Major benthic taxa							
				Pontoporeia		Oligochaeta		Sphaeriidae		Chironomidae	
1964	1972	1964	1972	1964	1972	1964	1972	1964	1972	1964	1972
4	12	14	14	0	0.1	20.4	12.3	4.8	3.2	<0.1	<0.1
11	1	19	22	2.0	4.8	7.2	11.3	2.6	1.1	0.3	0.1
50	66	19	21	4.2	0.3	5.4	8.2	7.6	0.6	0.2	0.1
59	60	19	20	0	<0.1	13.5	4.6	9.9	1.7	0.1	0.9
78	103	18	22	1.1	0.8	6.7	1.5	3.1	0.1	0.7	0.3
45	50	39	35	8.2	5.0	1.9	0.2	3.5	0.5	<0.1	<0.1
99	78	48	54	10.0	2.4	3.3	1.5	4.0	<0.1	<0.1	0
5	15	92	106	0.4	1.0	0.3	1.0	0.2	<0.1	0.3	<0.1
8	5	92	90	1.0	1.0	0.4	0.5	0.2	0	0.1	<0.1
57	62	92	87	1.7	0.4	0.9	0.1	0.6	0	0.3	0
38	38	92	99	1.8	0.6	1.0	0.2	0.2	0	0.2	0
71	85	183	167	0.4	0	0.8	0.1	0.1	0	0.2	0
65	75	225	223	0.5	0.2	0.4	0.1	<0.1	0	<0.1	0
Mean				2.4	1.5	4.8	3.2	2.8	0.6[a]	0.2	0.1[a]

[a]Abundances are significantly different (sign test; $P < 0.05$).

abundances reported by Kinney (1972) from a survey conducted during 1967–69 are shown with the 1964 and 1972 data (Table 7). Kinney did not give abundances at each of his 38 stations, but gave only mean abundances at each of three depth intervals. If the stations sampled in 1964 and 1972 are also grouped into the same depth intervals and abundances then compared, the Kinney data confirm the trend toward lower abundances of chironomids and sphaeriids after 1964.

In the early 1970s, both Canada and the United States enacted legislation to limit phosphorus in detergents and signed the Great Lakes Water Quality Agreement limiting phosphorus in the effluent of municipal waste treatment plants. Phosphorus is the most important limiting nutrient for summer phytoplankton production in the lake (Dobson et al. 1974; Sridharan and Lee 1977). As a result of these control measures, phosphorus loadings into Lake Ontario in the early 1980s were reduced by 39% and midlake spring concentrations of soluble reactive phosphorus were reduced by 33% (Stevens and Neilson 1987). While chlorophyll *a* concentrations did not decline, mean phytoplankton biomass in the early 1980s was reduced 43–58% compared with the early 1970s (Gray 1987). To determine whether corresponding changes occurred in benthic populations, the second comparison involved comparing data collected in 1964 (Hiltunen 1969) and in 1972 (Nalepa and Thomas 1976) with data collected during 1981–83 (Johannsson et al. 1985a) and 1985–87 (R. Dermott, Department of Fisheries and Oceans, Burlington, Ont., unpublished data). The latter two data sets are from the inclusive Bioindex Monitoring Program, Department of Fisheries and Oceans, Canada. As part of this program, benthic samples were regularly collected at three sites during 1981–83 and at two sites during 1985–87. Each of these sites (one or two profundal and one nearshore) was located near sites sampled in both 1964 and 1972. At the two profundal sites (>90 m), abundances of oligochaetes, sphaeriids, and chironomids in the 1980s were similar to abundances found in 1972, having remained lower than abundances found in 1964 (Table 8). Trends in abundances of *Pontoporeia* were not apparent; year-to-year fluctuations were high and trends at the two sites were inconsistent (Table 8).

Although benthic biomass estimates in the profundal are limited, data comparisons seem to suggest that a large decline in biomass occurred between the 1960s and the 1980s that is consistent with declines in abundances of many groups. In 1967–68, dry-weight biomass in the central profundal region was reported to be 2.12 $g \cdot m^{-2}$ (Johnson and Brinkhurst 1971); however, in the 1980s, mean dry-weight biomass was only 0.83 $g \cdot m^{-2}$ (Table 9). Declines in biomass were evident for all the major groups.

In addition to biomass, annual production of *Pontoporeia* in the profundal was determined in both 1967–68 (Johnson and Brinkhurst 1971) and in 1981–82 (Johannsson et al. 1985b). Production in 1967–68 was 1.59 $g \cdot m^{-2} \cdot yr^{-1}$ (this value is based on a given production rate of 0.025 $kcal \cdot m^{-2} \cdot d^{-1}$, a mean caloric content of 6.6 $cal \cdot mg^{-1}$, and an ash content of 15%), while production in 1981–82 was 1.86 $g \cdot m^{-2} \cdot yr^{-1}$. Thus, although biomass declined, production actually increased, resulting in an increase in the turnover rate (*P/B*) from about 0.9 in 1967–68 to about 2.2 in 1981–82. The turnover rate in 1967–68 might be considered more "typical" of profundal *Pontoporeia* populations; the value of 0.9 was generally similar to values reported from the profundal (65–115 m) of Lake Michigan in the late 1970s (Lubner 1979).

Trends in abundances of benthic populations at the nearshore site, located at a depth of about 28–35 m in the Kingston Basin, are given in Table 10. Included in this table are data from a recent study of benthic changes in the Bay of Quinte and adjacent waters of Lake Ontario between 1966 and 1984 (Johnson and McNeil 1986). This study documented changes in the benthos in response to phosphorus control measures in the 1970s. After point-source control of phosphorus became fully implemented in 1977, water quality, at least in the bay, improved almost immediately (Robinson 1986). In the Kingston basin, abundances of *Pontoporeia*, oligochaetes, and sphaeriids generally declined in the early 1980s when compared with abundances before 1977. Although in some years (1972 and 1982), differences between data sets were apparent, this trend was noted in the data of both Johnson and McNeil (1986) and in the comparative data of the other surveys (Hiltunen 1969; Nalepa

TABLE 7. Comparison between abundances (thousands per square metre) of major benthic taxa found in 1964 (Hiltunen 1969), 1967–69 (Kinney 1972), and 1972 (Nalepa and Thomas 1976) at each of three depth intervals.

	Shallow (<36 m)			Intermediate (36–90 m)			Deep (>91 m)		
Taxa	1964	1967–69	1972	1964	1967–69	1972	1964	1967–69	1972
Pontoporeia	2.1		2.1	9.1		2.1	1.3		0.8
Oligochaeta	8.6	5.5	8.4	2.6	1.7	4.7	0.8	0.4	0.4
Sphaeriidae	3.3	1.1	1.0	3.7	0.7	0.1	0.3	0.1	<0.1
Chironomidae	0.5	0.1	0.1	<0.1	<0.1	<0.1	0.2	0.1	<0.1
Gastropoda	0.3	0.2	0.2	<0.1	<0.1	<0.1	0	0	0

TABLE 8. Abundances (thousands per square metre) of major benthic taxa found in 1964, 1972, 1981–83, and 1985–87 at each of two profundal sites in Lake Ontario. 1964 = Station 18 (western profundal) and Station 38 (central profundal) (Hiltunen 1969); 1972 = Stations 5 and 10 (western profundal) and Stations 34, 38, and 46 (central profundal) (Nalepa and Thomas 1976); 1981, 1982, 1983 = Stations 12 (western profundal) and Station 41 (central profundal) (Johannsson et al. 1985a); 1985, 1986, 1987 = Station 41 (central profundal) (R. Dermott, unpublished data).

	Year							
	1964	1972	1981	1982	1983	1985	1986	1987
Western profundal (91–114 m)								
Pontoporeia	3.4	0.6			1.4			
Oligochaeta	1.0	0.3			0.4			
Sphaeriidae	0.6	0.0			<0.1			
Chironomidae	0.3	<0.1			<0.1			
Central profundal (91–126 m)								
Pontoporeia	1.8	1.4	2.1	2.3	1.3	2.4	2.1	2.1
Oligochaeta	1.0	0.3	0.4	0.4	0.3	0.3	0.5	0.4
Sphaeriidae	0.2	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1
Chironomidae	0.2	<0.1	<0.1	0.0	0.0	<0.1	<0.1	<0.1

TABLE 9. Comparisons between dry-weight biomass (milligrams per square metre) of the major benthic taxa found in 1967–68 (Johnson and Brinkhurst 1971), 1981–83 (Johannsson et al. 1985a), and 1985–87 (R. Dermott, unpublished data). Sampling site was in the main basin of the lake (>100 m). In the Johnson and Brinkhurst study, ash-free dry weight was converted to dry weight by assuming an ash content of 15%.

	Year						
Taxa	1967–68	1981	1982	1983	1985	1986	1987
Pontoporeia	1.73	0.80	0.80	0.50	1.14	0.43	0.58
Oligochaeta	0.36	0.11	0.10	0.06	0.17	0.15	0.13
Sphaeriidae	0.02	<0.01	<0.01	<0.01	0.01	<0.01	<0.01
Chironomidae	0.01	<0.01	0.0	0.0	<0.01	<0.01	<0.01
Total	2.12	0.90	0.90	0.56	1.32	0.58	0.71

and Thomas 1976; Johannsson et al. 1985a). Continued sampling since 1985, however, seems to indicate a reversal of earlier trends (Table 10). Abundances of all three groups have increased to levels not found since 1964. Trends in biomass were generally similar to those of abundances except for *Pontoporeia* (Table 11). While abundances of this species after 1985 were generally similar to abundances prior to 1977, biomass values were only one half as great. For the two time periods when annual production of *Pontoporeia* was estimated, 1967–68 and 1981–82, mean production was 9.3 and 5.2 $g \cdot m^{-2} \cdot yr^{-1}$ respectively, and turnover rates were 2.0 and 1.8.

Discussion

Although trends in the benthic fauna of Lake Ontario prior to the mid-1960s cannot be established, there is strong evidence suggesting that populations have changed since the 1960s. As noted by Nalepa (1987), one should be cautious when assessing trends in populations based on data from distinctly different surveys separated in time, but comparisons of several surveys have indicated a decline in both abundances and biomass of benthic populations, particularly at profundal depths. Reasons for this decline are not clearly defined. Typically, changes in benthic populations in deep lakes have been attributed to trends in water column productivity (Saether 1980); standing stocks of the benthos are directly related to the amount of food material settling from the water column. Yet, benthic populations in Lake Ontario declined in the late 1960s/early 1970s at a time when nutrients levels (and likely productivity) continued to increase (Stevens and Neilson 1987). Also, abundances in the 1980s have remained similar to abundances found in the early 1970s although phytoplankton biomass has declined (Gray 1987). Fish predation can certainly affect populations of preferred prey items (Johnson and McNeil 1986; Nalepa 1987), but it is unlikely that fish predation played a major role in the decline of the profundal benthos in the early 1970s. In a 1972 survey, fish biomass at depths below 55 m in Lake Ontario was

TABLE 10. Comparison of abundances (thousands per square metre) of the major benthic taxa found by various surveys[a] in the Kingston Basin of Lake Ontario at a depth of 28–35 m.

	Year											
Taxa	1964	1967	1968	1972	1977	1981	1982	1983	1984	1985	1986	1987	1988
Pontoporeia		6.7	9.0	2.7	9.6		6.5	3.2	2.6				
Oligochaeta		0.5	1.0	0.8	3.3		0.6	0.6	0.4				
Sphaeriidae		1.8	2.4	1.0	3.6		3.6	0.4	0.2				
Chironomidae		0.4	0.4	0.2	0.4		0.3	<0.1	<0.1				
Pontoporeia	5.9			6.8		6.9	8.8	3.9		6.9	6.6	9.6	13.9
Oligochaeta	2.8			1.2		0.6	0.8	0.5		2.0	3.2	3.0	
Sphaeriidae	2.2			0.3		0.6	0.4	0.2		<0.1	1.4	2.5	
Chironomidae	0.4			<0.1		<0.1	0.0	<0.1		<0.1	<0.1	<0.1	

[a]Upper half: 1967–84 = Lake Ontario Index Station of Johnson and McNeil (1986). Lower half: 1964 = Station 85 and 89 of Hiltunen (1969); 1972 = Station 96 and 97 of Nalepa and Thomas (1976); 1981–1983 Station 81 of Johannsson et al. (1985a); 1985–88 = Station 81 of R. Dermott (unpublished data).

TABLE 11. Comparison of dry-weight biomass (grams per square metre) of the major benthic taxa found by various surveys[a] in the Kingston Basin of Lake Ontario at a depth of 28–35 m. In the Johnson and McNeil (1986) study, ash-free dry weight was converted to dry weight by assuming an ash content of 15%.

	Year									
Taxa	1967	1968	1977	1981	1982	1983	1984	1985	1986	1987
Pontoporeia	5.09	5.53	6.90		2.99	2.19	1.59			
Oligochaeta	0.16	0.18	0.83		0.52	0.32	0.20			
Sphaeriidae	0.17	0.28	0.18		0.37	0.16	0.05			
Chironomidae	0.15	0.05	0.01		0.05	0.01	0.01			
Total	5.57	6.04	7.92		3.93	2.68	1.85			
Pontoporeia				3.02	2.45	1.56		2.38	1.60	2.78
Oligochaeta				0.17	0.28	0.17		0.90	0.60	0.79
Sphaeriidae				0.14	0.03	0.02		0.12	0.10	0.10
Chironomidae				<0.01	0.0	<0.01		0.01	<0.01	<0.01
Total				3.33	2.76	1.75		3.41	2.30	3.67

[a]Upper half: 1967–84 = Lake Ontario Index Station of Johnson and McNeil (1986). Lower half: 1981–83 = Station 81 of Johannsson et al. (1985a); 1985–87 = Station 81 of R. Dermott (unpublished data).

relatively small and consisted mainly of alewife (*Alosa pseudoharengus*) and rainbow smelt (*Osmerus mordax*) (Christie and Thomas 1981). While these species feed on *Pontoporeia*, there were no significant trends in abundances of either species between the 1960s and early 1970s (Christie 1973, 1974).

Benthic trends in the shallower Kingston Basin are also difficult to explain. The decline in the abundance and biomass of oligochaetes and sphaeriids in the Kingston Basin between 1977 and 1984 was attributed to a decline in productivity as a result of phosphorus input reductions in adjacent Bay of Quinte (Johnson and McNeil 1986). Yet, after 1984, despite continued low phosphorus loadings, numbers of oligochaetes and sphaeriids have increased to levels found prior to phosphorus reductions and recent numbers of *Pontoporeia* are the highest ever recorded (Table 10). Trophic interactions in nearshore areas are complex and controlling influences on a particular component are not always apparent. For instance, although phosphorus loadings in the upper Bay of Quinte have remained low, phytoplankton biomass has recently increased; it was hypothesized that phytoplankton biomass was partly controlled by changes in fish predation on the benthos (Nicholls and Hurley 1989). Since the Kingston Basin is currently being monitored for trends in both water column productivity and fish standing stocks, future works will hopefully provide insights into reasons for recent changes in the benthic populations.

At both the profundal (midlake) and nearshore (Kingston Basin) sites, numbers of *Pontoporeia* have remained the same or increased since the 1960s, while biomass has declined. Thus, either the size structure of the population has shifted toward smaller individuals, or the weight per unit length has decreased. Information on the size structure of the population is not available, but such a shift would most likely be caused by an increase in fish predation (McDonald et al. 1990). In the profundal, as noted earlier, fish predation was minimal when the biomass decline occurred (late 1960s/early 1970s), while major changes in fish populations in the Kingston Basin during this period were not apparent (Christie et al. 1987). On the other hand, a comparison between length–weight relationships for *Pontoporeia* in 1967–68 and 1981–82 shows a major decline in the weight per unit length, along with a corresponding increase in the metabolic rate (Fig. 1).

Given the relatively high contaminant exposures and body burdens of the Lake Ontario benthos, it remains a question whether contaminants have induced any of the changes noted in the populations. While organisms may tolerate sublethal concentrations of toxicants over the short term, long-term exposures may invoke physiological, histological, and biochemical

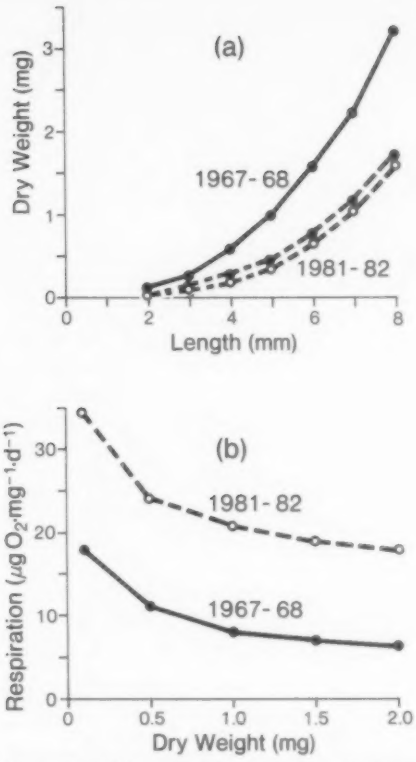


FIG. 1. (a) Length–weight relationship and (b) respiration rate of *Pontoporeia hoyi* in Lake Ontario in 1967–68 (Johnson and Brinkhurst 1971) and 1981–82 (Dermott and Corning 1988; Johannsson et al. 1985b). In the 1967–68 study, ash-free dry weight was converted to dry weight by assuming an ash content of 15%. Respiration rate calculated at 4°C. ●—●, 1967–68 (Kingston Basin); ○---○, 1981–82 (midlake). ●---●, 1981–82 (Kingston Basin). There was no difference in the respiration rate of *Pontoporeia* at the two 1981–82 sites (Johannsson et al. 1985b).

changes in the individual that may ultimately lead to changes at the population level. The organism requires energy to metabolize the toxicant and to replace or repair materials that have been damaged. Increased energy requirements for such nonproductive functions decrease the energy available for growth, given the same amount of energy intake. The decline in biomass of all the major macrobenthic groups in the profundal region in the 1960s corresponded to the time period when contaminant levels in the sediments were at an all-time peak in the 1960s and early 1970s (Durham and Oliver 1983) and may be a stress response manifested at the population level. In some groups, the decline in biomass coincided with a decline in numbers, but for *Pontoporeia*, lower biomass values can apparently be attributed to a decline in the weight per unit length of the individual. Weight loss has been observed in organisms exposed to sublethal levels of contaminants over a prolonged period (Keilty et al. 1988a). Inconsistent with the hypothesis that contaminants may have been a factor in the biomass decline, however, is the fact that contaminant levels have declined by the early 1980s (Durham and Oliver 1983), but standing stocks have remained lower than in the 1960s.

Summary of Research Needs

In addition to the research recommendations of previous reviews (Cook and Johnson 1974; Mozley 1990), and in view of the current status of the Lake Ontario macrobenthos, several immediate research needs have become apparent. The recent data sets available to examine long-term trends represent perhaps the longest record of benthic abundance and biomass in the Great Lakes. Nevertheless, these data have been collected from just a few sites. A lakewide survey is needed to document changes over a much broader area of the lake, and sampling sites should correspond as closely as possible to the sampling sites of previous surveys. Of particular interest are areas near major river mouths and along the southern shoreline east of the Niagara River.

Considering the relatively high concentrations of contaminants in the sediments and in the macrobenthos, studies to examine biochemical and physiological indicators of stress (Giesy et al. 1988) in Lake Ontario populations should be initiated. Comparative studies with organisms from the other Great Lakes would be useful in assessing relative impacts.

The effects of contaminants on the benthic community are difficult to assess from field measurements alone because of the complexity of the environment and the influences of natural events. In addition to examining community structure, assessments should include measures of contaminant concentrations and bioassays for acute and chronic impacts ("Sediment Quality Triad") (Chapman et al. 1987). Probably the most informative site to use this approach in Lake Ontario would be near the Niagara River mouth using *Pontoporeia* as the test organism.

Finally, the apparent discrepancy between pelagic inputs and benthic standing stocks in the profundal of Lake Ontario needs further attention. While the mass flux of organic material settling to the bottom has been quantified (Charlton 1983; Rosa 1985), information is needed on the nutritional value and source of these materials on a seasonal basis. The lipid composition of settling material can be useful in determining its food potential (Currie and Johns 1988; Gardner et al. 1989). Such information should further define the relationship between food inputs and benthic production and provide more realistic estimates of energy flow through the benthic system (i.e. Flint 1986). Conceivably, although the evidence seems to suggest otherwise, low benthic standing stocks in the profundal may be a result of high predation pressure by fish populations. Comparative studies using refined techniques such as manned submersibles (Eisenreich and Long 1989) or hydroacoustics (Burczynski and Johnson 1986) to estimate fish standing stocks are needed to put predation pressure in Lake Ontario in perspective.

NOTE ADDED IN PROOF: Since this article was written, the name *Pontoporeia hoyi* has been changed to *Diporeia* spp.

Acknowledgements

I thank R. Dermott for generously providing the unpublished data and W. S. Gardner, M. A. Quigley, M. G. Johnson, and an anonymous reviewer for their many useful suggestions on improving the manuscript.

References

ADAMSTONE, F. B. 1924. The distribution and economic importance of the bottom fauna of Lake Nipigon with an appendix on the bottom of Lake Ontario. Univ. Toronto Stud. Biol. Ser. 25: 34–100.

ALLAN, R. J., A. MUDROCH, AND A. SUDAR. 1983. An introduction to the Niagara River/Lake Ontario pollution problem. J. Great Lakes Res. 9: 111–117.

ALLEY, W. P., AND S. C. MOZLEY. 1975. Seasonal abundance and spatial distribution of Lake Michigan macrobenthos, 1964–67. Great Lakes Research Division Spec. Publ. 54, University of Michigan, Ann Arbor, MI. 103 p.

BARTON, D. R. 1986. Nearshore benthic invertebrates of the Ontario waters of Lake Ontario. J. Great Lakes Res. 12: 270–280.

BARTON, D. R., AND H. B. N. HYNES. 1978. Wave-zone macrobenthos of the exposed Canadian shores of the St. Lawrence Great Lakes. J. Great Lakes Res. 4: 27–45.

BARTONE, C. R., AND C. L. SCHELSKE. 1982. Lake-wide seasonal changes in limnological conditions in Lake Michigan in 1976. J. Great Lakes Res. 8: 413–427.

BORGMANN, U., AND D. M. WHITTLE. 1983. Particle-size conversion efficiency and contaminant concentrations in Lake Ontario biota. Can. J. Fish. Aquat. Sci. 40: 328–336.

BRINKHURST, R. O. 1970. Distribution and abundance of tubificid (Oligochaeta) species in Toronto Harbour, Lake Ontario. J. Fish. Res. Board Can. 27: 1961–1969.

BURCZYNSKI, J. J., AND R. L. JOHNSON. 1986. Application of dual-beam acoustic survey techniques to limnetic populations of juvenile sockeye salmon (*Oncorhynchus nerka*). Can. J. Fish. Aquat. Sci. 43: 1776–1788.

CAHILL, R. A. 1981. Geochemistry of recent Lake Michigan sediments. Ill. State Geol. Surv. Circ. 517: 1–96.

CARR, J. F., AND J. K. HILTUNEN. 1965. Changes in the bottom fauna of western Lake Erie from 1930–1961. Limnol. Oceanogr. 10: 551–569.

CHAPMAN, P. M., R. N. DEXTER, AND E. R. LONG. 1987. Synoptic measures of sediment contamination, toxicity and infaunal community composition (the Sediment Quality Triad) in San Francisco Bay. Mar. Ecol. Prog. Ser. 37: 75–96.

CHAPMAN, P. M., M. A. FARRELL, AND R. O. BRINKHURST. 1982a. Relative tolerances of selective aquatic oligochaetes to individual pollutants and environment factors. Aquat. Toxicol. 2: 47–67.

1982b. Relative tolerances of selected aquatic oligochaetes to combinations of pollutants and environmental factors. Aquat. Toxicol. 2: 69–78.

CHARLTON, M. N. 1983. Downflux of sediment, organic matter, and phosphorus in the Niagara River area of Lake Ontario. J. Great Lakes Res. 9: 201–211.

CHRISTIE, W. J. 1973. A review of the changes in the fish species composition of Lake Ontario. Great Lakes Fish. Comm. Tech. Rep. 23: 65 p.

1974. Changes in the fish species composition of the Great Lakes. J. Fish. Res. Board Can. 31: 827–854.

CHRISTIE, W. J., K. A. SCOTT, P. G. SLY, AND R. H. STRUS. 1987. Recent changes in the aquatic food web of eastern Lake Ontario. Can. J. Fish. Aquat. Sci. 44: 37–52.

CHRISTIE, W. J., AND N. A THOMAS. 1981. Biology, p. 327–340. *In* E. J. Aubert and T. L. Richards [ed.] IFYGL — The International Field Year for the Great Lakes. NOAA, Great Lakes Environ. Res. Lab., Ann Arbor, MI.

COOK, D. G., AND M. G. JOHNSON. 1974. Benthic macroinvertebrates of the St. Lawrence Great Lakes. J. Fish. Res. Board Can. 31: 763–782.

CURRIE, B. R., AND R. B. JOHNS. 1988. Lipids as indicators of the origin of organic matter in fine particulate matter. Aust. J. Mar. Freshwater Res. 39: 371–83.

DERMOTT, R., AND K. CORNING. 1988. Seasonal ingestion rates of *Pontoporeia hoyi* (Amphipoda) in Lake Ontario. Can. J. Fish. Aquat. Sci. 45: 1886–1895.

DOBSON, H. F. H., M. GILBERTSON, AND P. G. SLY. 1974. A summary and comparison of nutrients and related water quality in Lakes Erie, Ontario, Huron, and Superior. J. Fish Res. Board Can. 31: 731–738.

DURHAM, R. W., AND B. G. OLIVER. 1983. History of Lake Ontario contamination from the Niagara River by sediment radiodating and chlorinated hydrocarbon analysis. J. Great Lakes Res. 9: 160–168.

EADIE, B. J., R. L. CHAMBERS, W. S. GARDNER, AND GERALD L. BELL. 1984. Sediment trap studies in Lake Michigan: resuspension and chemical fluxes in the southern basin. J. Great Lakes Res. 10: 307–321.

EISENREICH, S. J., AND D. T. LONG. 1989. Submersible studies of biogeochemical and physical processes in Lake Superior. J. Great Lakes Res. 15: 1.

EVANS, M. S., R. W. BATHELT, AND C. W. RICE. 1982. PCBs and other toxicants in *Mysis relicta*. Hydrobiologia 93: 205–215.

FEE, E. J. 1973. A numerical model for determining integral primary production and its application to Lake Michigan. J. Fish. Res. Board Can. 30: 1447–1468.

FLINT, R. W. 1986. Hypothesized carbon flow through the deepwater Lake Ontario food web. J. Great Lakes Res. 12: 344–354.

FOX, M. E., J. H. CAREY, AND B. G. OLIVER. 1983. Compartmental distribution of organochlorine contaminants in the Niagara River and the western basin of Lake Ontario. J. Great Lakes Res. 9: 287–294.

FRANK, R., R. L. THOMAS, H. E. BRAUN, D. L. GROSS, AND T. T. DAVIES. 1981. Organochlorine insecticides and PCB in surficial sediments of Lake Michigan (1975). J. Great Lakes Res. 7: 42–50.

FRANK, R., R. L. THOMAS, H. E. BRAUN, J. RASPER, AND R. DAWSON. 1980. Organochlorine insecticides and PCB in the surficial sediments of Lake Superior (1973). J. Great Lakes Res. 6: 113–120.

FRANK, R., R. L. THOMAS, M. HOLDRINET, A. L. W. KEMP, AND H. E. BRAUN. 1979a. Organochlorine insecticides and PCB in surficial sediments (1968) and sediment cores (1976) from Lake Ontario. J. Great Lakes Res. 5: 18–27.

FRANK, R., R. L. THOMAS, M. HOLDRINET, A. L. W. KEMP, H. E. BRAUN, AND R. DAWSON. 1979b. Organochlorine insecticides and PCB in the sediments of Lake Huron (1969) and Georgian Bay and North Channel (1973). Sci. Total Environ. 13: 101–117.

GANNON, J. E., AND A. W. BEETON. 1969. Studies on the effects of dredged materials from selected Great Lakes harbors on plankton and benthos. Center for Great Lakes Studies Spec. Rep. 8, University Wisconsin-Milwaukee, Milwaukee, WI. p. 1–82.

GARDNER, W. S., B. J. EADIE, J. F. CHANDLER, C. C. PARRISH, AND J. M. MALCZYK. 1989. Mass flux and "nutritional composition" of settling epilimnetic particles in Lake Michigan. Can. J. Fish. Aquat. Sci. 46: 1118–1124.

GIESY, J. P., D. J. VERSTEEG, AND R. L. GRANEY. 1988. A review of selected clinical indicators of stress-induced changes in aquatic organisms. *In* M. S. Evans [ed.] Toxic contaminants and ecosystems health: a Great Lakes focus. Vol. 21. John Wiley and Sons, New York, NY.

GOLINI, V. I. 1979. Benthic macro- and meioinvertebrates of Lake Ontario 1977: distribution and relative abundance. Fish. Res. Board Can. Rep. Ser. MS No. 1519: 40 p.

GRAY, I. M. 1987. Differences between nearshore and offshore phytoplankton communities in Lake Ontario. Can. J. Fish. Aquat. Sci. 44: 2155–2163.

HANSON, J. M., AND R. H. PETERS. 1984. Empirical predictions of crustacean zooplankton and profundal macrobenthos biomass in lakes. Can. J. Fish. Aquat. Sci. 41: 439–445.

HART, D. R., P. M. MCKEE, A. J. BURT, AND M. J. GOFFIN. 1986. Benthic community and sediment quality assessment of Port Hope Harbour, Lake Ontario. J. Great Lakes Res. 12: 206–220.

HILTUNEN, J. K. 1969. The benthic macrofauna of Lake Ontario. Great Lakes Fish. Comm. Tech. Rep. 14: 39–50.

HOWMILLER, R. P., AND A. M. BEETON. 1971. Biological evaluation of environmental quality, Green Bay, Lake Michigan. J. Water Pollut. Control Fed. 43: 123–133.

JOHANNSSON, D. E., R. M. DERMOTT, R. FELDKAMP, AND J. E. MOORE. 1985a. Lake Ontario Long Term Biological Monitoring Program. 1981, 1982 Data Base. Can. Data Rep. Fish. Aquat. Sci. 552: 103 p.

1985b. Lake Ontario Long Term Biological Monitoring Program. Report for 1981 and 1982. Can. Tech. Rep. Fish. Aquat. Sci. 1414: 208 p.

JOHNSON, M. G., AND R. O. BRINKHURST. 1971. Production of benthic macroinvertebrates of Bay of Quinte and Lake Ontario. J. Fish. Res. Board Can. 28: 1699–1714.

JOHNSON, M. G., AND D. H. MATHESON. 1968. Macroinvertebrate communities of the sediments of Hamilton Bay and adjacent Lake Ontario. Limnol. Oceanogr. 13: 99–111.

JOHNSON, M. G., AND O. C. MCNEIL. 1986. Changes in abundance and species composition in benthic macroinvertebrate communities of the Bay of Quinte, 1966–84, p. 177–189. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

JUDD, J. H., AND J. G. BOCSOR. 1972. Effect of paper plant pollution and subsequent abatement on a littoral macroinvertebrate community in Lake Ontario: preliminary survey. Int. Assoc. Great Lakes Res. 15: 21–34.

KEILTY, T. J., D. S. WHITE, AND P. F. LANDRUM. 1988a. Sublethal responses to endrin in sediment by *Limnodrilus hoffmeisteri* (Tubificidae), and in mixed-culture with *Stylodrilus heringianus* (Lumbriculidae). Aquat. Toxicol. 13: 227–250.

1988b. Sublethal responses to endrin in sediment by *Stylodrilus heringianus* (Lumbriculidae) as measured by a ^{137}cesium marker layer technique. Aquat. Toxicol. 13: 251–270.

KINNEY, W. L. 1972. The macrobenthos of Lake Ontario. Int. Assoc. Great Lakes Res. 15: 53–79.

LANDRUM, P. F. 1988. Toxicokinetics of organic xenobiotics in the amphipod, *Pontoporeia hoyi*: role of physiological and environmental variables. Aquat. Toxicol. 12: 245–271.

LEE, A. H. 1972. Regional characterizations of the thermal properties of Lake Ontario. Int. Assoc. Great Lakes Res. 15: 625–634.

LUBNER, J. F. 1979. Population dynamics and production of the relict amphipod *Pontoporeia hoyi* at several Lake Michigan stations. Ph.D. thesis. University of Wisconsin, Milwaukee, WI. 98 p.

MAGNUSON, J. J., A. M. FORBES, AND R. J. HALL. 1976. An assessment of the environmental effects of dredged material disposal in Lake Superior, Final Report, Vol. 3. Duluth-Keweenaw study areas. Mar. Stud. Cent., University of Wisconsin, Madison, WI. 172 p.

MCDONALD, M. E., L. B. CROWDER, AND S. B. BRANDT. 1990. Changes in *Mysis* and *Pontoporeia* populations in southeastern Lake Michigan: a response to shifts in the fish community. Limnol. Oceanogr. 35: 220–227.

MOZLEY, S. C. 1990. Review of Lake Ontario benthic studies. *In* N. A. Thomas and W. J. Christie [ed.] Status of the biota of Lake Ontario. Great Lakes Fishery Commission and International Joint Commission. Spec. Publ. No. 88-2.

MOZLEY, S. C., AND R. P. HOWMILLER. 1977. Environmental status of the Lake Michigan region: zoobenthos of Lake Michigan. Argonne National Lab. Rep. No. ANL/ES-40. Vol. 6. U.S. Energy Research and Development Administration. 148 p.

MUDROCH, A. 1983. Distribution of major elements and metals in sediment cores from the western basin of Lake Ontario. J. Great Lakes Res. 9: 125–133.

NALEPA, T. F. 1987. Long-term changes in the macrobenthos of southern Lake Michigan. Can. J. Fish. Aquat. Sci. 44: 515–524.

1989. Estimates of macroinvertebrate biomass in Lake Michigan. J. Great Lakes Res. 15: 437–443.

NALEPA, T. F., AND P. F. LANDRUM. 1988. Benthic invertebrates and contaminant levels in the Great Lakes: effects, fates, and role in cycling, p. 77–102. *In* M. S. Evans [ed.] Toxic contaminants and ecosystem health: a Great Lakes focus. John Wiley and Sons, New York, NY.

NALEPA, T. F., M. A. QUIGLEY, AND R. W. ZIEGLER. 1988. Sampling efficiency of the Ponar grab in two different benthic environments. J. Great Lakes Res. 14: 89–93.

NALEPA, T. F., AND N. A. THOMAS. 1976. Distribution of macrobenthic species in Lake Ontario in relation to sources of pollution and sediment parameters. J. Great Lakes Res. 2: 150–163.

NICHOLLS, K. M., AND D. A HURLEY. 1989. Recent changes in the phytoplankton of the Bay of Quinte, Lake Ontario: the relative importance of fish, nutrients, and other factors. Can. J. Fish. Aquat. Sci. 46: 770–779.

PARKER, J. I., H. L. CONWAY, AND E. M. YAGUCHI. 1977. Seasonal periodicity of diatoms, and silicon limitation in offshore Lake Michigan, 1975. J. Fish. Res. Board Can. 34: 552–558.

POULTON, D. J., K. J. SIMPSON, D. R. BARTON, AND K. R. LUM. 1988. Trace metals and benthic invertebrates of nearshore Lake Ontario at Hamilton Harbour. J. Great Lakes Res. 14: 52–65.

POWERS, C. F., AND A. ROBERTSON. 1967. Design and evaluation of an all-purpose benthos sampler, p. 179–187. *In* J. C. Ayers and D. C. Chandler [ed.] Studies on the environment and eutrophication of Lake Michigan. Great Lakes Res. Div. Spec. Rep. 30, University of Michigan, Ann Arbor, MI.

RASMUSSEN, J. B., AND J. KALFF. 1987. Empirical models for zoobenthic biomass in lakes. Can. J. Fish. Aquat. Sci. 44: 990–1001.

ROBERTSON, A., AND W. P. ALLEY. 1966. A comparative study of Lake Michigan macrobenthos. Limnol. Oceanogr. 11: 576–583.

ROBINSON, G. W. 1986. Water quality of the Bay of Quinte, Lake Ontario, before and after reductions in phosphorus loading, p. 50–58. *In* C. K. Minns [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

ROSA, F. 1985. Sedimentation and sediment resuspension in Lake Ontario. J. Great Lakes Res. 11: 13–25.

SAETHER, O. 1980. The influence of eutrophication on deep lake benthic invertebrate communities. Prog. Water Technol. 12: 161–180.

SCHELSKE, C. L., AND J. C. ROTH. 1973. Limnological survey of Lakes Michigan, Superior, Huron and Erie. Great Lakes Res. Div. Publ. Univ. Mich. 17: 108 p.

SCHNEIDER, J. C., F. F. HOOPER, AND A. M. BEETON. 1969. The distribution and abundance of benthic fauna in Saginaw Bay, Lake Huron. Int. Assoc. Great Lakes Res. 12: 80–90.

SHIOMI, M. T., AND V. K. CHAWLA. 1970. Nutrients in Lake Ontario. Int. Assoc. Great Lakes Res. 13: 715–732.

SMITH, W. E. 1972. Culture, reproduction, and temperature tolerance of *Pontoporeia affinis* in the laboratory. Trans. Am. Fish. Soc. 101: 253–256.

SMITH, V. E., J. M. SPURR, J. C. FILKINS, AND J. J. JONES. 1985. Organochlorine contaminants of wintering ducks foraging on Detroit River sediments. J. Great Lakes Res. 11: 231–246.

SRIDHARAN, N., AND G. F. LEE. 1977. Algal nutrient availability and limitation in Lake Ontario during IFYGL. Part III. Algal nutrient limitation in Lake Ontario during IFYGL. U.S. Environ. Protect. Agency, Ecol. Res. Serv., EPA-600/3-77-046a: 46.

STADELMANN, P., AND A. FRASER. 1974. Phosphorus and nitrogen cycle on a transect in Lake Ontario during the International Field Year 1972–73. Int. Assoc. Great Lakes Res. 17: 92–107.

STADELMANN, P., J. E. MOORE, AND E. PICKETT. 1974. Primary productivity in relation to temperature structure, biomass concentration, and light conditions at an inshore and offshore station in Lake Ontario. J. Fish. Res. Board Can. 31: 1215–1232.

STEVENS, R. J. J. 1987. A review of Lake Ontario water quality with emphasis on the 1981–82 intensive years. Report to the Surveillance Work Group, International Joint Commission. 342 p.

STEVENS, T. J., AND M. A. NEILSON. 1987. Response of Lake Ontario to reductions in phosphorus load, 1967–82. Can. J. Fish. Aquat. Sci. 44: 2059–2068.

THOMAS, R. L. 1983. Lake Ontario sediments as indicators of the Niagara River as a primary source of contaminants. J. Great Lakes Res. 9: 118–124.

THOMAS, R. L., AND C. I. DELL. 1978. Sediments of Lake Superior. J. Great Lakes Res. 4: 264–275.

THOMAS, R. L., A. L. W. KEMP, AND C. F. M. LEWIS. 1972. Distribution, composition, and characteristics of the surficial sediments of Lake Ontario. J. Sediment. Petrol. 42: 66–84.

WHITTLE, D. M., AND J. D. FITZSIMONS. 1983. The influence of the Niagara River on contaminant burdens of Lake Ontario biota. J. Great Lakes Res. 9: 295–302.

Present Status and Temporal Trends of Organochlorine Contaminants in Young-of-the-Year Spottail Shiner (*Notropis hudsonius*) from Lake Ontario

K. Suns and G. Hitchin

Aquatic Biology Section, Ontario Ministry of the Environment, Rexdale, Ont. M9W 5L1, Canada

and E. Adamek[2]

Laboratory Services Branch, Ontario Ministry of the Environment, Rexdale, Ont. M9W 5L1, Canada

Suns, K., G. Hitchin, and E. Adamek. 1991. Present status and temporal trends of organochlorine contaminants in young-of-the-year spottail shiner (*Notropis hudsonius*) from Lake Ontario. Can. J. Fish. Aquat. Sci. 48: 1568–1573.

Contaminant residue data from Ontario nearshore collections of young-of-the-year spottail shiner (*Notropis hudsonius*) were used to assess present status and temporal trends of bioavailable organochlorine contaminants in Lake Ontario. PCB residues in spottail shiners were in excess of the International Joint Commission Aquatic Life Guideline at 11 of the 14 sites sampled in 1987; mirex residues exceeded the Guideline at 7 of the 14 sites sampled. PCB and total DDT residues in the recent shiner collections were significantly ($p < 0.01$) lower relative to residue levels in collections in the 1970's. However, residue declines have slowed during the 1980's. Thus, PCB residues in spottail shiners declined by 69% over a 5-yr interval (1975–80) whereas residues declined only by 17% at the same sites during the following 7-yr interval (1980–87). Residues of hexachlorobenzene, heptachlor, aldrin, total hexachlorocyclohexane, octachlorostyrene, total chlordane, and toxaphene were generally near their detection limits in all shiner collections. A Forage Fish Contaminant Index was established for the purpose of ranking the collection sites in relative order of contamination to assess the need for point-source investigations.

Des données sur les résidus de contaminants dans des queues à tâche noire (*Notropis hudsonius*) de moins d'un an recueillies près des rives dans le lac Ontario ont été utilisées pour évaluer les concentrations actuelles et l'évolution des concentrations des contaminants organochlorés pouvant être absorbés par les organismes vivants dans le lac Ontario. À 11 des 14 endroits ayant fait l'objet d'échantillonnages en 1987, les concentrations des résidus de BPC excédaient les normes établies en matière de vie aquatique par la Commission mixte internationale; dans le cas du mirex, cette proportion était de 7 endroits sur 14. Les résidus de BPC et de DDT total dans les échantillons récents de queues à tâche noire étaient significativement ($p < 0,01$) moins abondants que dans les échantillons des années 1970. Cependant, il y a eu ralentissement du taux de réduction des résidus au cours des années 1980. En effet, les résidus de BPC dans les queues à tâche noire ont chuté de 69 % dans l'espace de 5 ans de 1975 à 1980, mais durant les 7 années suivantes, soit de 1980 à 1987, cette réduction n'était plus que de 17 % aux mêmes endroits. Dans tous les poissons de cette espèce échantillonés, la teneur des résidus d'hexachlorobenzène, d'heptachlor, d'aldrine, d'hexachlorocyclohexane total, d'octachlorostyrène, de chlordane total eet de toxaphène se situait généralement près des seuils de détection de ces résidus. Un indice de contamination du poisson fourrage a été établi afin de classer les sites d'échantillonnage suivant leur taux de contamination, ce qui permettra d'établir les besoins en matière d'études ponctuelles.

Received January 24, 1989
Accepted June 26, 1990
(JA028)

Reçu le 24 janvier 1989
Accepté le 26 juin 1990

Although concern for Great Lakes toxicants has existed for several decades, the growing interest in the sport fishery has created a new awareness for toxic contaminant management. Recent categorization of Lake Ontario toxicants under the Lake Ontario Toxics Management Plan (1988) has placed eight compounds in a high-risk category, seven of them organics. Likewise, 9 of the 11 critical pollutants on the International Joint Commission (IJC) Priority List are organics. While the primary concerns about persistent aquatic contaminants are associated with human health protection, there are interrelated concerns about wildlife and environmental health in general.

In the absence of reliable contaminant loading data and analytical difficulties in quantifying lipophilic compounds in the water column, biota have been used increasingly to assess contaminant trends and the biological availability of contaminants. A contaminants surveillance program initiated by the Ontario Ministry of the Environment (OME) in 1975 introduced young-of-the-year spottail shiner (*Notropis hudsonius*) as a nearshore biomonitor for spatial and temporal trend assessment. Shiners are restricted to nearshore habitat and have undifferentiated food habits; therefore, young-of-the-year spottail shiner contaminant residues reflect site-specific contaminant availability from waterborne sources.

TABLE 1. Organochlorine residues (ng·g wet weight^{-1}, mean ± SD) in young-of-the-year spottail shiner from selected sites of Lake Ontario. NA = not available; ND = not detected; TR = trace.

Sampling site	Year sampled	No. of samples	Fish size (mm)	% fat	ΣPCB	ΣDDT	Mirex
Niagara-on-the-Lake	1975	5	56 ± 4	2.3 ± 0.3	690 ± 195	244 ± 52	NA
	1977	7	51 ± 3	2.5 ± 0.6	654 ± 170	157 ± 38	13 ± 4
	1978	8	51 ± 1	1.9 ± 0.2	320 ± 49	99 ± 49	29 ± 8
	1979	8	50 ± 2	2.4 ± 0.4	153 ± 23	26 ± 9	TR
	1980	7	56 ± 2	2.1 ± 0.4	266 ± 51	41 ± 9	11 ± 2
	1981	7	55 ± 3	1.9 ± 0.1	327 ± 62	73 ± 15	10 ± 3
	1982	5	53 ± 3	2.2 ± 0.4	255 ± 24	82 ± 14	6 ± 2
	1983	6	59 ± 5	2.5 ± 0.5	136 ± 55	TR	ND
	1984	6	58 ± 4	2.2 ± 0.2	273 ± 107	71 ± 23	10 ± 6
	1985	7	54 ± 7	2.8 ± 0.3	127 ± 38	13 ± 13	ND
	1987	7	60 ± 4	2.6 ± 0.3	116 ± 18	34 ± 9	7 ± 3
Twelve Mile Creek	1975	5	58 ± 5	5.2 ± 0.9	890 ± 319	98 ± 46	NA
	1978	8	51 ± 3	2.9 ± 0.4	349 ± 63	88 ± 17	20 ± 12
	1979	8	51 ± 4	2.1 ± 0.4	271 ± 49	66 ± 19	ND
	1980	7	48 ± 6	1.9 ± 0.3	148 ± 28	50 ± 10	TR
	1981	6	54 ± 5	2.5 ± 0.5	205 ± 15	93 ± 32	TR
	1982	7	41 ± 5	1.6 ± 0.3	279 ± 26	33 ± 22	21 ± 5
	1983	7	64 ± 3	3.2 ± 0.4	236 ± 47	48 ± 6	8 ± 4
	1984	6	54 ± 4	2.0 ± 0.3	267 ± 45	100 ± 31	7 ± 5
	1985	4	57 ± 10	2.5 ± 0.7	337 ± 100	65 ± 19	ND
	1986	4	51 ± 7	2.2 ± 0.2	321 ± 97	138 ± 43	ND
	1987	7	60 ± 3	2.2 ± 0.2	207 ± 36	85 ± 13	12 ± 2
Burlington Beach	1977	9	55 ± 4	5.3 ± 0.7	833 ± 106	267 ± 36	9 ± 2
	1980	7	47 ± 6	2.7 ± 0.2	250 ± 54	46 ± 11	TR
	1983	7	57 ± 4	4.5 ± 0.7	375 ± 68	40 ± 12	7 ± 2
	1985	7	41 ± 3	1.8 ± 0.5	502 ± 128	29 ± 22	ND
	1987	5	47 ± 2	2.6 ± 0.2	194 ± 20	47 ± 6	7 ± 3
Credit River	1976	10	62 ± 3	2.8 ± 0.5	1315 ± 578	278 ± 106	32 ± 13
	1978	8	60 ± 3	2.6 ± 0.3	590 ± 53	96 ± 12	28 ± 3
	1979	8	56 ± 3	3.7 ± 0.6	186 ± 28	70 ± 12	ND
	1980	7	62 ± 4	2.7 ± 0.6	238 ± 59	59 ± 20	TR
	1982	7	52 ± 7	3.2 ± 0.2	183 ± 27	66 ± 32	7 ± 2
	1983	7	60 ± 8	4.1 ± 1.5	329 ± 46	23 ± 11	5 ± 2
	1987	7	65 ± 3	3.7 ± 0.6	258 ± 10	91 ± 7	37 ± 11
Humber River	1977	8	62 ± 3	7.3 ± 0.4	2218 ± 263	268 ± 32	5 ± 2
	1978	8	58 ± 5	5.8 ± 0.5	2938 ± 391	406 ± 99	15 ± 4
	1979	8	60 ± 6	4.0 ± 1.3	1223 ± 347	76 ± 12	ND
	1980	6	62 ± 5	4.0 ± 0.4	621 ± 66	41 ± 4	ND
	1981	6	62 ± 5	5.0 ± 0.8	954 ± 45	86 ± 41	ND
	1982	6	58 ± 2	3.7 ± 0.4	353 ± 70	28 ± 20	ND
	1983	7	68 ± 3	5.2 ± 0.4	537 ± 122	48 ± 7	ND
	1985	7	64 ± 3	5.9 ± 0.7	524 ± 152	48 ± 21	ND
	1987	6	66 ± 3	5.2 ± 0.6	235 ± 33	31 ± 4	ND
Detection limits					20	1	5

Since the nearshore cyprinids are important forage fish in the Great Lakes (Scott and Crossman 1973), and contaminant concentrations are often higher in the nearshore waters (Swackhamer and Armstrong 1987), the role of forage fish in contaminant transfer to higher trophic levels should not be understated. This paper will summarize the current status of bioavailable organochlorine residues in Ontario waters of Lake Ontario and selected temporal trend data for a 12-yr interval (1975–87). The focus will be on total PCB, DDT, DDT metabolites, and mirex. A preliminary assessment will be made of the effects of contaminant accumulations in spottail shiner in terms of wildlife protection criteria and guidelines.

Methods

Young-of-the-year spottail shiners (mean lengths 41–65 mm in various years, Table 1) were collected annually during the month of September from the nearshore waters of Lake Ontario (Fig. 1) using a bag seine. Individual fish were measured for total lengths (TL) and wrapped as 10 fish composites in hexane-rinsed aluminum foil and frozen. Samples were stored at −20°C before analyses. Whole-fish homogenates for each composite sample were analyzed for contaminant residues and lipid content. Residues were identified and quantified at the Ontario Ministry of the Environment laboratory in Rexdale. Packed col-

FIG. 1. Young-of-the-year spottail shiner collection sites in Lake Ontario.

umn gas chromatography was used for PCB, hexachlorobenzene, heptachlor, mirex, aldrin, octachlorostyrene, *p,p'*-DDE and *p,p'*-DDD, while capillary gas chromatography was used for chlordane, hexachlorocyclohexane, *o,p'*-DDT, and *p,p'*-DDT (Ontario Ministry of the Environment 1981).

Detection limits were 20 $ng \cdot g^{-1}$ for PCBs, 5 $ng \cdot g^{-1}$ for mirex, 1 $ng \cdot g^{-1}$ for DDT, 2 $ng \cdot g^{-1}$ for chlordane, 1 $ng \cdot g^{-1}$ for hexachlorobenzene, and 1 $ng \cdot g^{-1}$ for octachlorostyrene.

Since the Niagara River is considered to be a major source of organic contaminants to Lake Ontario (Whittle and Fitzsimons 1983), spottail shiner data from the Niagara-on-the-Lake collections were included in this report. Site selection for temporal trend assessment was based on the requirement that at least 5 yr of data be available, including some of the earlier collections from the 1970's. Only 5 of the 14 sites sampled met these criteria (Table 1). Student *t*-tests and straight line regression analysis were used to determine statistical significance. To compare changes of contaminant accumulations between the 1970's and 1980's, data from the following collection years were used to determine end-points for calculating rates of change: 1975–77, 1980–82 and 1985–87.

Results and Discussion

PCBs

Higher PCB residues were generally found in spottail shiners from western Lake Ontario, and the data showed that individual watersheds had a strong influence on PCB availability in the nearshore. PCB accumulations in shiners in 1987 exceeded the IJC Aquatic Life Guideline of 100 $ng \cdot g^{-1}$ (Great Lakes Water Quality Agreement 1978) at 11 of the 14 Lake Ontario sites sampled (Fig. 2). While the atmosphere has been considered to be an important source of PCBs, with estimates for Lake Ontario ranging from 180 to 300 $kg \cdot yr^{-1}$ (Thomann and DiToro 1983; Eisenreich et al. 1981), there is no evidence in the nearshore shiner data that atmospheric inputs of PCBs play a dominant role. If atmospheric inputs were the major source, PCB residue levels would be more uniformly distributed among the collection sites for a given region. Major differences in PCB availability were apparent from the residue spatial distribution, suggesting site-specific inputs (Fig. 2). We concluded that site-specific inputs continued to govern PCB availability in the nearshore. To maintain PCB residue levels in the nearshore forage fish below the IJC Aquatic Life Guideline, it may be necessary to further reduce watershed-associated PCB inputs to Lake Ontario.

PCB accumulations in recent spottail shiner collections (1980–87) were significantly ($p < 0.01$) lower than those from

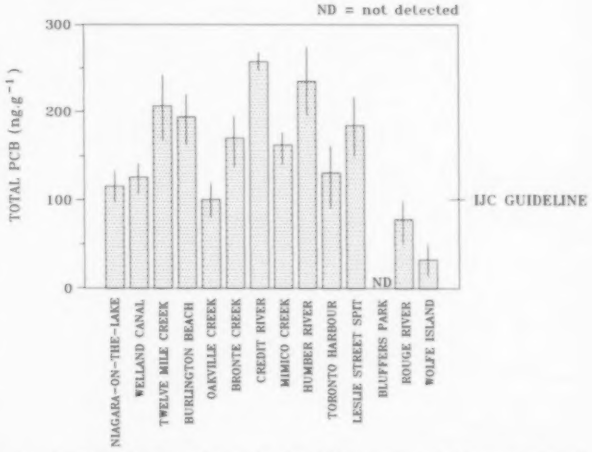


FIG. 2. Total PCB residues in the 1987 young-of-the-year spottail shiner collections from Lake Ontario. Values are composite sample arithmetic means with 95% confidence limits.

the 1970's prior to 1977 (Table 1; Fig. 3). These residue declines coincided with the basinwide ban of PCB use in the early 1970's implemented by all jurisdictions on the Great Lakes. However, PCB residue reductions have slowed considerably since the early 1980's at all Lake Ontario sites sampled when compared with the 5-yr interval (1975–80) in the late 1970's. Whereas residue reductions ranged from 69 to 84% for all sites sampled during 1975–80, PCB residues in the Twelve Mile Creek and Credit River collections increased during 1980–87. These findings suggest recent increases in PCB availability and should be considered for further investigations. Lake means for PCB residue rates of change were found to be similar for Lakes Ontario (17%), Erie (11%), and St. Clair (17%) (OME, unpublished data). While it is generally assumed that the lipid content in fish influences organochlorine contaminant accumulation, lipid-adjusted residue values in this data set did not significantly alter the trend results, nor explain the annual fluctuations of PCB residues.

Mirex

The highest mirex accumulations were found in the Credit River and Wolfe Island shiner collections, both of which had significantly ($p < 0.01$) higher mirex levels than other collections from Lake Ontario (Fig. 4). Historically, mirex residues in spottail shiner from the western parts of Lake Ontario have been similar and their spatial distribution has supported the assumption that the Niagara River is one of the two sources of

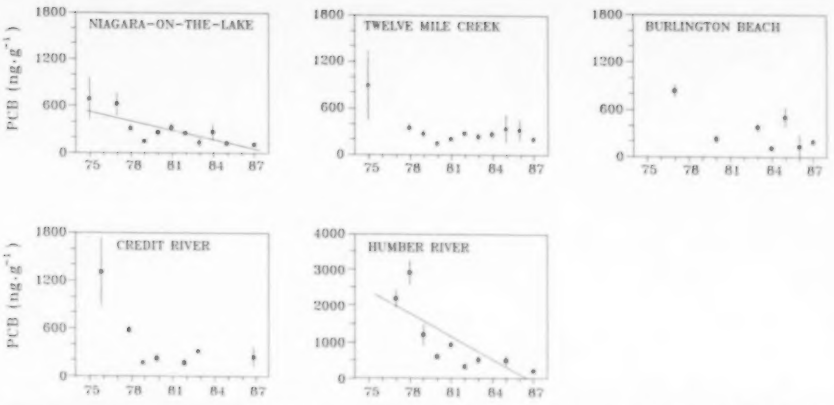


FIG. 3. Total PCB residue trends in Lake Ontario young-of-the-year spottail shiner. Values are composite sample arithmetic means with 95% confidence limits. Regression lines indicate a significant ($p < 0.05$) change over time.

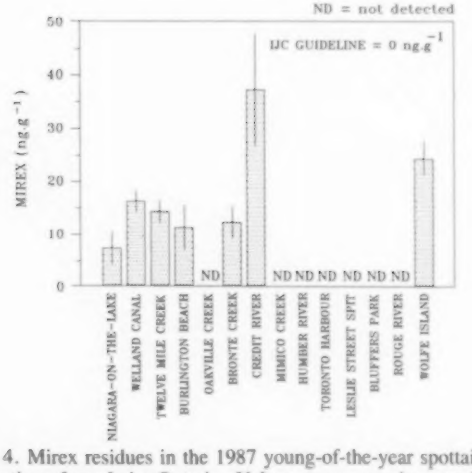


FIG. 4. Mirex residues in the 1987 young-of-the-year spottail shiner collections from Lake Ontario. Values are composite sample arithmetic means with 95% confidence limits.

mirex to Lake Ontario (Environment Canada 1977; Pickett and Dossett 1979). However, mirex residue distribution in the 1987 shiner collections has been anomalous and may suggest a local source at the Credit River. Further work in source identification may proceed pending the evaluation of fish residue data from the 1988 Credit River collections. Low concentrations of mirex have been present in Wolfe Island spottail shiner since 1982, and these residues may be associated with mirex inputs from the Oswego River (Scrudato and Del Prete 1982). However, reasons for the sudden residue increase in 1987 are not known. Mirex residue data have not increased measurably in the Oswego River spottail shiner collections (L. Skinner, New York State Department of Environmental Conservation, pers. comm.). Mirex residues exceeded the IJC Aquatic Life Guideline at 7 of the 14 sites sampled in 1987 (Fig. 4).

Since mirex levels in spottail shiner have fluctuated considerably, and concentrations have been near their detection limits (Table 1), the assessment of temporal trends was obscured (Fig. 5). Nevertheless, mirex residues decreased in the Niagara-on-the-Lake and Twelve Mile Creek collections during the 1980's.

DDT and Metabolites

Although DDT metabolite residues were found in all of the 1987 shiner collections, residues in all samples were below the New York State Department of Environmental Conservation Fish Flesh Criterion of 200 $ng \cdot g^{-1}$ (Fig. 6; Newell et al. 1987).

Metabolite *p,p'*-DDE was the principal compound found in most of the Lake Ontario shiner, generally constituting from 81 to 100% of the total DDT residue. These values are somewhat higher than data reported for the United States where *p,p'*-DDE constituted about 70% of the total DDT (Schmitt et al. 1985). Metabolite *p,p'*-DDD was higher in the Mimico Creek, Humber River, and Toronto Inner Harbour collections, constituting from 40 to 63% of the total DDT residue. The presence of *p,p'*-DDD indicates a more recent use of DDT, since it is a less stable compound than *p,p'*-DDE (Aguilar 1984).

Total DDT residues in the recent (1987) spottail shiner collections were significantly ($p < 0.01$) lower than residues in comparable samples from the 1970's (Fig. 7). These substantial residue decreases appeared to be associated with the basin-wide ban of DDT use in the early 1970's. Unlike the relatively uniform lakewide rates of change for PCB's, total DDT residue declines in shiner for a 7-yr period (1980–87) were variable: Lake Ontario 18%; Lake Erie 42% and Lake St. Clair 50% (OME, unpublished data). Since *p,p'*-DDE clearance rates are considerably higher than those of PCB's (Norstrom et al. 1985), it may be concluded that the low rate of change for DDT residues in Lake Ontario suggests more recent inputs.

Other Organochlorines

Residues of hexachlorobenzene, heptachlor, aldrin, total hexachlorocyclohexane, octachlorostyrene, total chlordane, and toxaphene were generally near their detection limits in shiner collections from Lake Ontario.

Forage Fish Contaminant Index

To prioritize compounds and rank collection sites for further investigations, the 1987 spottail shiner residue data were used to develop a Forage Fish Contaminant Index. The index was derived by summing ratios from fish contaminant concentration/guideline concentration calculations, thereby providing a more realistic basis for water quality assessment than evaluat-

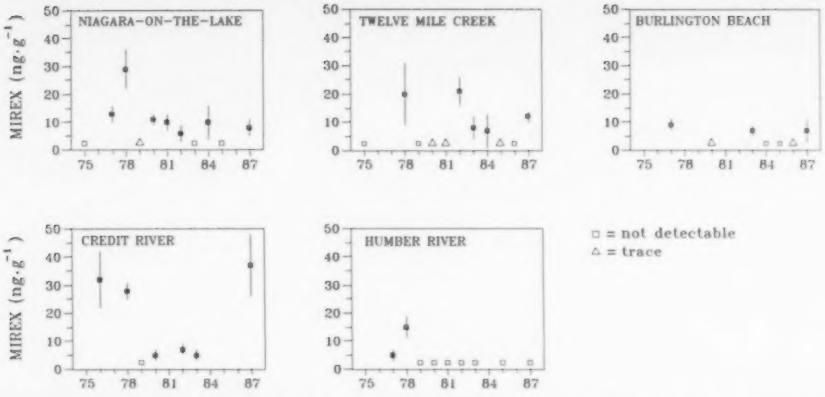


FIG. 5. Mirex residue trends in Lake Ontario young-of-the-year spottail shiner. Values are composite sample arithmetic means with 95% confidence limits.

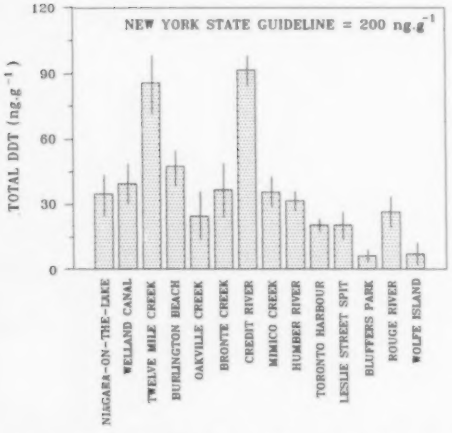


FIG. 6. Total DDT residues in the 1987 young-of-the-year spottail shiner collections from Lake Ontario. Values are composite sample arithmetic means with 95% confidence limits.

ing individual compounds (Table 2). Bishop (1989) has shown that the sum-total of organochlorine body burdens rather than specific compounds was related to biological effects. Guidelines or objectives used for the index were either the IJC Aquatic Life Guidelines (Great Lakes Water Quality Agreement 1978) or the New York State Department of Environmental Conservation Fish Flesh Criteria (Newell et al. 1987). However, guidelines were only available for six of the compounds analyzed in this survey; therefore, only a partial assessment of the total body burden of contaminants is offered.

Credit River, Wolfe Island, and Welland Canal sites were ranked as the most polluted, with mirex and PCBs as the principal contaminants of concern. Both compounds were also categorized as priority pollutants under the Lake Ontario Toxics Management Plan (1988), based on lakewide assessment of sportfish residue data. Total DDT, chlordane, hexachlorobenzene, and octachlorostyrene also contributed marginally to shiner contamination but their residue levels never exceeded any of the available guidelines or objectives. Further developmental work is necessary to establish additional guidelines for other bioaccumulative compounds to arrive at a comprehensive contaminant index.

Conclusions

The spatial distribution of PCB residues in spottail shiner has shown that elevated PCB availability in Lake Ontario nearshore

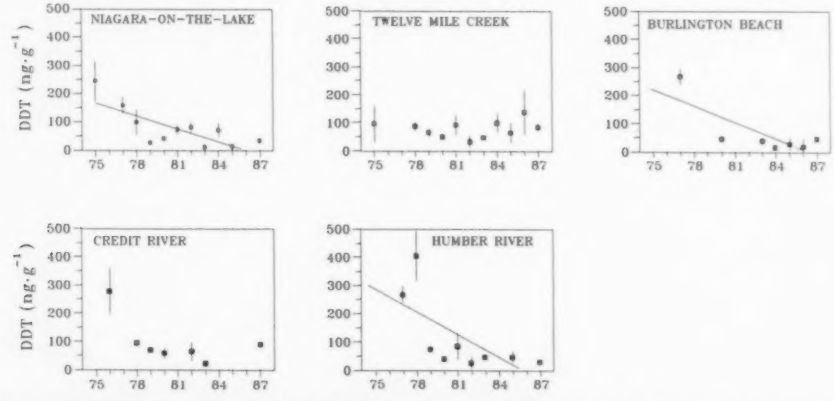


FIG. 7. Total DDT residue trends in Lake Ontario young-of-the-year spottail shiner. Values are composite sample arithmetic means with 95% confidence limits. Regression lines indicate a significant ($p < 0.05$) change over time.

TABLE 2. Forage Fish Contaminant Index (FFCI) for Lake Ontario (1987) young-of-the-year spottail shiner.

Site No.	Sampling site	ΣPCB		Mirex		ΣDDT		ΣChlordane		Hexachlorobenzene		Octachlorostyrene		FFCI sum of ratios	Rank
		ng·g^{-1}	Ratio	ng·g^{-1}	Ratio	ng·g^{-1}	Ratio	ng·g^{-1}	Ratio	ng·g^{-1}	Ratio	ng·g^{-1}	Ratio		
1	Niagara-on-the-Lake	116	1.2	7	7.0	34	0.1	1	0.0	3	0.0	0	0.0	8.3	7
2	Welland Canal	127	1.3	14	14.0	39	0.2	1	0.0	0	0.0	0	0.0	15.5	3
3	Twelve Mile Creek	207	2.1	12	12.0	85	0.4	1	0.0	2	0.0	1	0.1	14.6	4
4	Burlington Beach	194	1.9	7	7.0	47	0.2	2	0.0	0	0.0	0	0.0	9.1	6
5	Bronte Creek	171	1.7	12	12.0	36	0.1	1	0.0	0	0.0	0	0.0	13.8	5
6	Oakville Harbour	101	1.0	0	0.0	24	0.1	2	0.0	0	0.0	0	0.0	1.1	12
7	Credit River	258	2.6	37	37.0	91	0.5	1	0.0	2	0.0	2	0.1	40.2	1
8	Mimico Creek	163	1.6	0	0.0	35	0.2	19	0.0	1	0.0	2	0.1	1.9	10
9	Humber River	235	2.4	0	0.0	31	0.1	9	0.0	2	0.0	1	0.1	2.6	8
10	Toronto Inner Habour	132	1.3	0	0.0	20	0.1	4	0.0	0	0.0	0	0.0	1.4	11
11	Leslie Street Spit	185	1.9	0	0.0	20	0.1	0	0.0	0	0.0	0	0.0	2.0	9
12	Bluffers Park	0	0.0	0	0.0	6	0.0	4	0.0	0	0.0	0	0.0	0.0	14
13	Rouge River	78	0.8	0	0.0	26	0.1	1	0.0	0	0.0	0	0.0	0.9	13
14	Wolf Island	33	0.3	24	24.0	7	0.0	0	0.0	2	0.0	0	0.0	24.3	2
Guideline/objective (ng·g^{-1})		100[a]		1[b]		200[c]		500[c]		330[c]		20[c]			

[a]IJC Aquatic Life Guideline (Great Lakes Water Quality Agreement 1978).
[b]The IJC Aquatic Life Guideline value is 0; the value 1 was used to derive a ratio $< \infty$.
[c]New York State Department of Environmental Conservation Fish Flesh Criteria for Piscivorous Wildlife (Newell et al. 1987).

is site specific. This observation has support in temporal trend assessments where site-specific changes in PCB residue reduction rates have occurred. Therefore we conclude that PCB inputs to the Lake Ontario nearshore exist. Since the majority (79%) of the 1987 shiner collections had PCB accumulations in excess of the IJC Aquatic Life Guideline, the watershed-associated PCB inputs should be further reduced.

While mirex residues were in excess of the IJC Aquatic Life Guideline in 50% of the 1987 shiner collections, there was no evidence of local inputs except the Credit River and Wolfe Island anomalies. Residue data from the 1987 Niagara-on-the-Lake collections showed that mirex inputs from the Niagara River continue. Whether mirex accumulations in the nearshore shiner were primarily influenced by sediment-borne residues or current inputs is not known.

The usefulness of the Forage Fish Contaminant Index in its present format is limited due to its partial assessment only of the contaminant burden. Therefore, additional criteria development and expanded analytical capabilities at the congener–isomer level are needed for some of the principal compounds to arrive at a comprehensive index.

Acknowledgements

The authors acknowledge the financial support provided under the Canada–Ontario Agreement for Great Lakes Water Quality (1986). We thank R. Howard of the Laboratory Services Branch for processing the fish and M. Barclay and R. Di Clemente for typing the manuscript. We are also indebted to W. Scheider, J. Ralston, C. Schenk, and A. Johnson for their valuable comments and constructive review of the manuscript.

References

AGUILAR, A. 1984. Relationship of DDE/DDT in marine mammals to the chronology of DDT input to the ecosystem. Can. J. Fish. Aquat. Sci. 41: 840–844.

BISHOP, C. 1989. Hatchability and deformities in populations of snapping turtles. Presented at the Workshop on Cause–Effect Linkages, Chicago, Illinois, 1989. International Joint Commission, Windsor, Ont.

EISENREICH, S. J., B. B. LOONEY, AND J. D. THORNTON. 1981. Airborne organic contaminants in the Great Lakes ecosystem. Environ. Sci. Technol. 15: 30–38.

ENVIRONMENT CANADA. 1977. Mirex in Canada. Report of the Task Force on Mirex to the Joint Department of Environment and National Health and Welfare Committee on Environmental Contaminants. Environment Canada, Ottawa, Ont.

GREAT LAKES WATER QUALITY AGREEMENT. 1978. Agreement with annexes and terms of references between the United States of America and Canada. International Joint Commission, Windsor, Ont.

LAKE ONTARIO TOXICS MANAGEMENT PLAN. 1988. Categorization of toxics in Lake Ontario. Toxics Categorization Workgroup, International Joint Commission, Windsor, Ont. 5 p.

NEWELL, A. J., D. W. JOHNSON, AND L. K. ALLEN. 1987. Niagara River Biota Contamination Project: fish flesh criteria for piscivorous wildlife. N.Y. State Dep. Environ. Conserv. Tech. Rep. 87-3.

NORSTROM, R. J., T. P. CLARK, AND D. V. WESELOH. 1985. Great Lakes monitoring using herring gulls. Hazardous contaminants in Ontario. Human and environmental effects, p. 86–92. *In* T. C. Hutchinson and S. M. Evans [ed.] Proc. of Workshop, March 7–8, 1985. Institute for Environmental Studies, University of Toronto, Toronto, Ont.

ONTARIO MINISTRY OF THE ENVIRONMENT. 1981. Handbook analytical methods for environmental samples. Laboratory Services Branch, Ontario Ministry of the Environment, Toronto, Ont. 159 p.

PICKETT, R. L., AND D. A. DOSSETT. 1979. Mirex and the circulation of Lake Ontario. J. Physiol. Ocean. 9: 441–445.

SCHMITT, C. J., J. L. ZAJICEK, AND M. A. RIBICK. 1985. National Pesticide Monitoring Program: residues of organochlorine chemicals in freshwater fish, 1980–81. Arch. Environ. Contam. Toxicol. 14: 225–260.

SCOTT, W. G., AND E. J. CROSSMAN. 1973. Freshwater fishes of Canada. Bull. Fish. Res. Board Can. 184: 461 p.

SCRUDATO, R. J., AND A. DEL PRETE. 1982. Lake Ontario sediment–mirex relationships. J. Great Lakes Res. 8: 695–699.

SWACKHAMER, D. L., AND D. E. ARMSTRONG. 1987. Distribution and characterization of PCBs in Lake Michigan Water. J. Great Lakes Res. 13: 24–36.

THOMANN, R. V., AND D. M. DITORO. 1983. Physico-chemical model of toxic substances in the Great Lakes. J. Great Lakes Res. 9: 474–495.

WHITTLE, D. M., AND J. D. FITZSIMONS. 1983. The influence of the Niagara River on contaminant burdens of Lake Ontario biota. J. Great Lakes Res. 9: 295–302.

Rehabilitation of Lake Ontario: the Role of Nutrient Reduction and Food Web Dynamics

John H. Hartig

International Joint Commission, Great Lakes Regional Office, 100 Ouellette Ave., Windsor, Ont. N9A 6T3, Canada

James F. Kitchell

Center for Limnology, University of Wisconsin, Madison, WI 53706, USA

Donald Scavia

Great Lakes Environmental Research Laboratory, National Oceanic and Atmospheric Administration, 2205 Commonwealth Blvd., Ann Arbor, MI 48105, USA

and Stephen B. Brandt

Chesapeake Biological Laboratory, University of Maryland, Solomons, MD 20688, USA

Hartig, J. H., J. F. Kitchell, D. Scavia, and S. B. Brandt. 1991. Rehabilitation of Lake Ontario: the role of nutrient reduction and food web dynamics. Can. J. Fish. Aquat. Sci. 48: 1574–1580.

The Laurentian Great Lakes have a complex history of changes due to eutrophication, invasion of exotic species, and fisheries and phosphorus management practices. Remedial actions have reduced nutrient loadings and enhanced the role of food web interactions in improving water quality. Workshops sponsored through the United States – Canada International Joint Commission have addressed the relative importance of nutrient abatement and/or food web manipulation in affecting water quality trends. Both controls have combined to enhance water clarity in Lake Michigan. Lake Ontario has already exhibited the effects of nutrient controls and may be on the verge of manifesting food web controls. Research and monitoring recommendations to elucidate the effects of nutrient and food web controls include the following: (1) water quality and fisheries agencies must coordinate monitoring activities, standardize techniques, and establish and maintain long-term data sets to evaluate the effects of water quality and fisheries programs separately and together; (2) controlled, mesoscale, whole-system experiments should be performed to quantify rates (e.g. growth, predation, etc.) of food web interactions; and (3) the scientific community should promote research which quantifies the impact of changes in food web dynamics on changes in toxic substance levels in Great Lakes fishes.

Au cours de leur histoire, les Grands Lacs Laurentiens ont été transformés par l'eutrophisation, l'invasion d'espèces exotiques et par la manière dont les phosphates et les pêches ont été gérés. Des mesures correctives ont permis de réduire l'accumulation de nutriments et mis en valeur le rôle des interactions trophiques dans l'amélioration de la qualité de l'eau. Des ateliers parrainés par la Commission mixte internationale États-Unis – Canada ont traité de l'importance de réduire la quantité de nutriments dans ces eaux ou d'agir sur le réseau alimentaire pour les assainir. Ces deux types d'action ont permis de rendre plus pur les eaux du lac Michigan. Les effets des mesures de réduction des nutriments se sont déjà faits sentir dans le lac Ontario et on s'apprête à y agir sur le réseau alimentaire. Voici certaines recommandations en matière de recherche et de surveillance visant à améliorer notre connaissance des effets des mesures de contrôle des nutriments et du réseau alimentaire : 1) les organismes responsables de la qualité des eaux et des pêches doivent coordonner leurs activités de surveillance, normaliser leurs méthodes et établir et maintenir des ensembles de données à long terme leur permettant d'évaluer séparément ou ensemble les effets de la qualité de l'eau et des programmes portant sur les pêches; 2) des expériences contrôlées à échelle moyenne et de type holistique devraient être menées de façon à quantifier les taux (de croissance, de prédation, etc.) des interactions ayant lieu dans le réseau alimentaire et 3) la communauté scientifique doit promouvoir les recherches visant à quantifier l'impact des modifications de la dynamique du réseau alimentaire sur les concentrations des substances toxiques présentes dans les poissons des Grands Lacs.

Received January 25, 1989
Accepted June 26, 1990
(JA037)

Reçu le 25 janvier 1989
Accepté le 26 juin 1990

In the past 10 yr, two management strategies have evoked dramatic effects in the Great Lakes: phosphorus management and fishery management. The 1972 Great Lakes Water Quality Agreement adopted a phosphorus management strategy to control nuisance algal problems in the lower lakes and maintain the oligotrophic state of the upper lakes. Phosphorus loadings to the Great Lakes have decreased substantially (e.g. approximately a 13 000 tonne (t) decrease to Lake Erie since 1972) and resulted in dramatic improvements, particularly in Saginaw Bay and the lower Great Lakes (Hartig and Gannon 1986). Simultaneously, the fishery interests (Great Lakes Fishery Commission or GLFC) implemented a strategy to control

the parasitic sea lamprey (*Petromyzon marinus*) which provided an opportunity to stock Pacific salmon and native trout. Over the past 10 yr, salmon stocking in the Great Lakes has increased substantially (e.g. over 15 million salmon and trout stocked in Lake Michigan in 1984), resulting in a sport fishery worth an estimated $2–4 billion per annum (Talhelm 1987). Fundamental management questions include the following: are phosphorus management and fishery management strategies compatible? Will nutrient reductions limit fish production? Can predator stocking, through trophic cascading effects (Carpenter et al. 1985), alter planktonic communities and, ultimately, water quality indicators?

To address these questions requires an understanding of the linkages between management strategies and ecosystem changes. To help identify the effects of phosphorus abatement (i.e. nutrient control) and salmonine stocking (i.e. food web control via predation) on Lake Michigan, the Science Advisory Board of the International Joint Commission (IJC) hosted the 1985 Food Web I Workshop which focused on an evaluation of the relationship between recent improvements in water quality and the current changes in biological community structure. Lake Michigan historical data documented the decrease in alewife (*Alosa pseudoharengus*) abundance that coincided with increased stocking of piscivores and increases in abundance of native species such as bloaters (*Coregonus hoyi*) and yellow perch (*Perca flavescans*) (Kitchell and Crowder 1986). Large-sized *Daphnia* also increased in abundance during summer. Concomitantly, total phosphorus loadings and in-lake concentrations decreased, while water clarity increased substantially (Scavia et al. 1986).

The Food Web I Workshop concluded that nutrient abatement probably had reduced open-lake phosphorus levels in Lake Michigan in winter which, in turn, reduced the amount of spring phytoplankton and spring chlorophyll (Kitchell et al. 1988). Salmon predation likely initiated a cascade effect in which reduced alewife abundance caused an increase in abundance of large-sized *Daphnia* in open waters. The higher rates of grazing by these *Daphnia* on phytoplankton led to increased summer water clarity. For further information on the Food Web I Workshop, see Kitchell et al. (1988). A more extensive history of food web changes in Lake Michigan is presented in Scavia et al. (1986), Kitchell and Carpenter (1987), and Scavia and Fahnenstiel (1987).

Subsequent to the Food Web I Workshop, the IJC hosted the 1987 Food Web II Workshop which focused on food web dynamics in Lake Ontario. Lake Ontario was chosen because its phosphorus and salmon stocking trends were following those in Lake Michigan, and Lake Ontario would probably be the next Great Lake to manifest the effects of food web control. The purpose of this paper is to present a summary of the conclusions and recommendations from the Food Web II Workshop.

Food Web II Workshop

Approximately 40 scientists with expertise on Lakes Ontario and Michigan took part in the Food Web II Workshop. The workshop began with a series of presentations on long-term empirical data sets from Lake Ontario followed by presentations on how such information could be interpreted and used to manage large lakes using a whole-system approach. Two groups (i.e. nutrient controls and food web controls) were formed to answer specific questions related to trends and possible causes. The groups then came together to discuss and debate their findings and reach consensus on conclusions and recommendations. Presented below are the major conclusions on limnological changes in Lake Ontario, a comparison of the recent changes in the physicochemical and biological characteristics of Lakes Ontario and Michigan, and the consensus recommendations from workshop participants. More detailed information on the Food Web II Workshop and the abstracts and data presented at the workshop can be found in IJC (1987a).

Limnological Changes in Lake Ontario

Evaluation of trends in Lake Ontario's food web proved to be difficult because in certain areas the data were limited and in others there have not been dramatic changes in recent years. Based on the review of the available data from 1970 to 1985 (IJC 1987a), the following conclusions were drawn:

(1) Total phosphorus loads have decreased by 80% since 1972 and are approaching the target set by the Great Lakes Water Quality Agreement.

(2) Winter–spring total phosphorus (P) decreased slowly from the 1971 high of approximately 25 $\mu g \cdot L^{-1}$ and then more dramatically after 1977; the current concentration is near 14 $\mu g \cdot L^{-1}$. During the same time period, summer epilimnetic total P decreased only from approximately 17 to 15 $\mu g \cdot L^{-1}$. Nitrate concentrations continue to increase, as is the case in most of the other Great Lakes (IJC 1987b). In Lake Ontario, increasing nitrogen (N) and decreasing P concentrations have resulted in winter–spring total nitrogen/total phosphorus (TN/TP) ratios that increased from about 16 in 1977 to over 32 in 1982. N/P ratios continue to increase annually.

(3) Summer epilimnetic chlorophyll concentrations have not changed over the period of analysis, although some evidence exists to suggest that algal biomass has decreased. There also appear to be recent shifts in algal species composition, including the disappearance of potentially N-fixing blue-greens and an increase in the relative proportion of small species.

(4) No major changes in water clarity (e.g. Secchi disc transparency) have been observed in recent years.

(5) A comparison of zooplankton community structure and abundance from 1981 to 1985 with that of earlier studies (1967–72) found no detectable change in the range of abundances or community composition between the two periods. This is consistent with Taylor et al. (1987) who found no marked change in zooplankton during the 1970s. Few changes were observed during the 1980s, based on the internally consistent analysis of BIOINDEX stations (a Lake Ontario long-term biological monitoring program established by the Department of Fisheries and Oceans (Canada)).

(6) Lake Ontario zooplankton size structure and species composition seem strongly regulated by heavy alewife predation.

(7) Alewife abundance has varied considerably year-to-year, since it increased after the major 1976–77 die-off; however, no clear trend in abundance is obvious after 1980 (O'Gorman et al. 1987). In recent years, alewives have generally been in poor condition.

(8) Slimy sculpin (*Cottus cognatus*) and, perhaps, rainbow smelt (*Osmerus mordax*) populations in the Kingston basin have declined as lake trout (*Salvelinus namaycush*) stocking has increased there (Christie et al. 1987a).

(9) Coho (*Oncorhynchus kisutch*) and chinook salmon (*O. tshawytscha*) stocking in Lake Ontario increased from 40 000 in 1968 to 5 415 000 in 1984.

(10) Significant piscivore effects (predator control) are not broadly demonstrated in Lake Ontario. Some recent reductions in slimy sculpin density and the condition of adult chinook salmon have been observed, but longer time series and larger spatial coverage are needed. Recently, food web – nutrient interactions have been identified as an important factor in water quality improvements in Lake Ontario's Bay of Quinte (Minns et al. 1987).

(11) Recent reductions in phosphorus loading and open-lake phosphorus concentration do not appear to be limiting fish production.

The phytoplankton trend data suggest a rather stable period, with only subtle changes in algal species composition. This has occurred during the more obvious decreases in TP and increase in TN concentrations (see IJC 1987b). The lack of correlation between TP and chlorophyll (Stevens and Neilson 1987) changes seem linked to Lake Ontario's light climate and TN/TP ratio. Model analyses of Lake Ontario during the early 1970s indicated that the lake became nitrogen limited by summer's end (Thomann et al. 1975; Scavia 1979, 1980). Because winter–spring TN/TP has only recently crossed the threshold of 29 set by a cross-sectional analysis of several lakes (Smith 1983) for transition from nitrogen-limited to phosphorus-limited lakes, it is likely that until about 1982–83, Lake Ontario's summer phytoplankton potentially were limited by nitrogen. Only after those years would further decreases in TP result in decreased phytoplankton biomass or chlorophyll. TP decreases after 1983 have been slight compared with the 1977–82 period. Thus, chlorophyll changes should continue to be small.

It appears that the subsurface light climate in Lake Ontario may also play a significant role in the apparent lack of correlation between TP decreases and phytoplankton changes. Summer penetration depth of 1% of surface light reaches only 9–10 m, which is 1–2 m short of the mixing depth. Therefore, Lake Ontario phytoplankton may also be limited by the availability of light during much of the year.

There also appears to be an uncoupling (i.e. components behave relatively independently) of phytoplankton and zooplankton in the open waters of Lake Ontario. This notion comes from two sources. The first is based on correlations between the abundance of edible algae (defined by size of extant cells) and measures of zooplankton production (e.g. egg ratios) Except for a few daphnid species, this correlation is very low, indicating that this size range of algae is perhaps not the direct nutrition of all zooplankton. A second line of reasoning derives from comparison of algal size spectra in relation to the preferred food sizes of the dominant zooplankton. While a shift to smaller phytoplankton sizes has been noted in recent years, the dominant forms until then have been relatively large compared with the preferred size for the dominant small zooplankton, *Bosmina* spp.

It was suggested that the still relatively high phosphorus concentrations allow the large algal forms to persist, leading to a size mismatch of zooplankton and their food supply. Food web influence may also be important if size-selective predation by alewife structures the zooplankton size spectrum toward small species. An alternative hypothesis is that predation by alewife forced size structure toward these smaller *Bosmina*, and their removal of smaller algal cells resulted in the shift toward more grazing-resistant, larger algal cells. Among Lake Ontario's offshore zooplankton, little evidence of change over the past decade suggests that size-selective predation by zooplanktivorous fishes (primarily alewife) and/or invertebrate predators is the major cause of apparent uncoupling between herbivores and the phytoplankton–nutrient interactions. However, without more information concerning the relative rates of algal and zooplankton production and loss in Lake Ontario, it is difficult to establish causality of food web and nutrient controls at the phytoplankton–zooplankton interface.

Alewife is a critically important species in the Lake Ontario food web. It forms the primary prey of all species of adult salmonines (Brandt 1986), is an efficient size-selective zooplanktivore that has the ability to dramatically alter zooplankton abundance and community structure, and has been shown to impact recovery of native species (e.g. predation on yellow perch larvae; Brandt et al. 1987). Yet the key factors which apparently control alewife abundance (recruitment variabilities, predation, overwinter mortality) are not understood. Alewife relative abundance has not declined steadily in Lake Ontario during recent years. Although salmon stocking in Lake Ontario has increased to the point where total number stocked per unit area or per unit volume is much higher than in the other Great Lakes, significant predation effects are not yet broadly demonstrated.

What directions might Lake Ontario take under nutrient and grazing control? If phytoplankton are phosphorus limited, then further reductions in winter–spring TP should result in lower summer epilimnetic phytoplankton biomass or chlorophyll concentrations; however, as TP reductions will likely be small as phosphorus target loads are approached, a more reasonable expectation is one of small changes in phytoplankton density accompanied by subtle species shifts. Shifts will likely be toward smaller species and perhaps a larger percentage of diatoms in summer as the silicon/phosphorus (Si/P) ratio increases. As TP continues to decrease, primary production may also decrease, with consequential reductions in grazer biomass (zooplankton and benthos); however, those changes will again be slight and perhaps undetectable with current methods. Overall, trends tied to effects of TP reductions will probably be slow, small, and subtle.

If there is a dramatic decrease in alewife abundance due to food web influences or high winter mortality, and other major planktivores do not replace alewife, then we may expect certain abrupt changes similar to those observed in Lake Michigan. There may be shifts to large zooplankton body size within the extant assemblage, followed by species shifts to larger organisms as intraspecific plasticity reaches limits. Larger body size and greater per capita grazing rates could evoke a reduction in algal biomass. While decreases in algal biomass could also follow nutrient reduction, mean algal cell size would likely shift to larger, less edible species under grazer control rather than to smaller species expected under nutrient control. Release from alewife planktivory should be accompanied by released benthivory and a possible increase in vulnerable benthic prey.

Intensive salmon stocking is relatively recent. Predator effects on alewife stocks may not be apparent until the end of this decade, and then perhaps only as a depensatory (constant amount per predator) agent acting in conjunction with density-independent mortality (Kitchell and Crowder 1986). In any event, salmon stocking rates are and have been such that if predation effects are to occur, they should be manifest within the next few years.

Expected shifts in community structure caused by salmonine predation would be a reduction in the size and abundance of zooplanktivores which form the main prey of salmonines and a corresponding increase in the size spectra upon which these

zooplanktivores feed. One might expect a decrease in the abundance of target zooplanktivores, an increase in the abundance of large species of zooplankton such as *Daphnia* spp., and an increase in abundance of nonprey fishes such as lake herring (*Coregonus artedii*), yellow perch, and white perch (*Morone americana*). Shifts in fish growth rates and condition would be expected as prey abundances change. Future effects of predaceous *Bythotrephes* sp., a recent invader, cannot be predicted, although preliminary evidence suggests that *Bythotrephes* sp. can quickly dominate the dynamics of zooplankton populations, but its influence may subside equally rapidly (Lehman 1988). A new exotic, the zebra mussel (*Dreissena polymorpha*), has recently appeared in Lake Ontario. Its dramatic effects on water clarity in western Lake Erie suggest that water quality changes in Lake Ontario may include effects from a complexity of grazing activities (J. H. Leach, Ontario Ministry of Natural Resources, pers. comm.).

Lake Ontario – Lake Michigan Comparison

Most of the workshop participants' expectations for Lake Ontario were derived from observed changes in Lake Michigan, but it was well recognized that the Lake Michigan data are largely corollary in nature and are confounded by cooccurring perturbations and that Lake Michigan and Lake Ontario species complements and sampling methods differ. In Lake Michigan, phosphorus abatement probably reduced winter open-lake phosphorus levels which, in turn, reduced the amount of spring phytoplankton and spring chlorophyll (Kitchell et al. 1988). Salmon predation likely initiated a cascade effect in which reduced alewife abundance caused an increase in abundance of large-sized *Daphnia* in open waters. Higher grazing rates by these *Daphnia* on phytoplankton led to increased summer water clarity.

However, these food web effects observed in Lake Michigan have not been broadly manifest in Lake Ontario (Table 1). Several aspects of Lake Ontario's ecology and limnology are different from those of Lake Michigan. These may be substantial enough to result in different responses of the Lake Ontario ecosystem to similar stimuli (Table 2). Some of the notable differences include the following:

(1) Lake Ontario has a much smaller silica reserve in winter, which likely limits spring diatom production there more severely than in Lake Michigan. The dominance of spring net diatom production in Lake Michigan may be an important precursor for subsequent grazer control in the summer epilimnion.

(2) During summer stratification, Lake Ontario's primary production is limited to the epilimnion (mixing depth 11–12 m; 1% light at 9–10 m) whereas a substantial portion of Lake Michigan's summer production is below the thermocline (mixing depth 10 m; 1% light at 27–33 m).

(3) Lake Ontario's zooplankton community has a sizeable population of invertebrate grazers (e.g. *Cyclops, Diacyclops*) that were not important in Lake Michigan, and their influence on the zooplankton community, should vertebrate predation be released, is not known.

(4) Lake Ontario zooplankton is presently dominated by *Bosmina*, a small cladoceran, rather than by the calanoid copepod *Diaptomus* spp. that dominated Lake Michigan's summer population before the rise of *Daphnia*.

(5) Based on paleolimnology, it appears that Lake Michigan long-term algal succession never progressed beyond conditions found in the early 1900s in Lake Ontario. Thus, entirely different Lake Ontario responses are possible.

TABLE 1. Comparison of Lake Michigan's and Lake Ontario's recent trends in indicators of change.

	Lake Michigan	Lake Ontario
Salmonids	Annual stocking of coho and chinook salmon has increased from 660 000 in 1966 to 10 664 000 in 1984	Annual stocking of coho and chinook salmon has increased from 40 000 in 1968 to 5 415 000 in 1984
Planktivores	Alewife (the dominant zooplanktivore) abundance decreased by 80–90% between the mid-1970s and the early 1980s	The size of the alewife population fluctuated widely between 1977 and 1986 because of two weather-related die-offs (die-offs in winters of 1976–77 and 1983–84)
Zooplankton	*Daphnia pulicaria*, a relatively large cladoceran, was first observed in autumn 1978 and became the summer dominant in 1983	Limited data available. A comparison of zooplankton community structure and abundance from 1981 to 1985 with that of earlier studies (1967–72) found no detectable change in the range of abundances or community composition between the two periods
Phytoplankton	Historical studies suggest changes in species composition. Spring chlorophyll *a* concentrations decreased slightly between 1976 and 1984. No dramatic change in summer chlorophyll *a* concentration between 1976 and 1984	Between the late 1960s and early 1980s there has been a change in species composition toward more species indicative of mesotrophic and oligotrophic conditions and an increase in abundance of small species
Water transparency	Summer Secchi disc depths increased from 4–5 m in mid-1960s to 15 m or greater in the early 1980s	No apparent trend between the late 1960s and early 1980s
Phosphorus concentration	A slight decrease in mean annual total phosphorus concentration from approximately 7 $\mu g \cdot L^{-1}$ in 1976 to approximately 4 $\mu g \cdot L^{-1}$ in 1985	Spring, midlake total phosphorus concentration has decreased from a maximum of 30.6 $\mu g \cdot L^{-1}$ in 1973 to 10.7 $\mu g \cdot L^{-1}$ in 1985
Phosphorus loading	A decrease in municipal total phosphorus loading from 2325 $t \cdot yr^{-1}$ in 1975 to 894 $t \cdot yr^{-1}$ in 1985	A decrease in municipal total phosphorus loading from 9860 $t \cdot yr^{-1}$ in 1972 to 1710 $t \cdot yr^{-1}$ in 1985

TABLE 2. Municipal total phosphorus loadings ($t \cdot yr^{-1}$) and annual stocking (thousands) of coho and chinook salmon in Lakes Michigan and Ontario. Phosphorus data were obtained from IJC (1987b) and salmon stocking data were obtained from M. Dakota (Great Lakes Fishery Commission, Ann Arbor, MI, pers. comm.).

	Phosphorus loadings		Salmon stocking	
Year	Michigan	Ontario	Michigan	Ontario
1966	—	—	660	—
1967	—	—	2534	—
1968	—	—	1888	40
1969	—	—	3998	309
1970	—	—	5447	580
1971	—	—	5068	520
1972	—	9860	4782	969
1973	—	—	5251	1208
1974	—	—	6809	1843
1975	2325	4220	6785	1958
1976	2336	3082	6580	936
1977	1660	3089	6064	352
1978	1314	2728	8050	674
1979	1224	2898	9028	999
1980	1047	2512	9049	1283
1981	934	2208	7198	1843
1982	885	2115	8493	2557
1983	960	1903	8903	3547
1984	894	1894	10664	5415
1985	894	1710	9137	4293

Despite such differences, workshop participants felt that harbingers of Lake Ontario food web effects should resemble those observed in Lake Michigan. Two classes of evidence parallel the sequence of events in Lake Michigan. First, Lake Ontario zooplankton size structure and species composition seem strongly regulated by heavy alewife predation. Second, slimy sculpin and, perhaps, rainbow smelt populations in the Kingston basin have declined as lake trout stocking has increased there. A similar decline of slimy sculpin, presumably due to predation by stocked lake trout, occurred in Lake Michigan prior to the major decline of alewife. Given that salmonine consumption levels in the lake as a whole have not yet peaked, we may be on the verge of seeing predation effects. Alewives are generally in poor condition and winters have not yet been severe during times of high salmonine predation rates. Large *Daphnia* populations (e.g. *D. pulicaria*) are the key component of a suite of changes that should result if and as alewife stocks are reduced by piscivores.

Research and Monitoring Needs

While it is clear that more and better information concerning the processes and mechanisms controlling Lake Ontario's ecosystem is needed, certain strategic research and monitoring efforts can be identified which specifically address the issues of interactions and synergisms of food web and nutrient controls. A list of some strategic research and monitoring needs follows:

(1) Seasonal progression of phytoplankton should be monitored and nutrient and light limitation established.

(2) The causes of the relatively slow decrease (on annual scales) of summer epilimnion TP concentrations and the increase (on seasonal scales) of those concentrations over spring values should be evaluated. These dynamics may be critical in the evaluation of nitrogen, phosphorus, and light limitation of phytoplankton growth.

(3) Algal growth and loss rates should be determined. If a mismatch in algal size and zooplankton preferred food size exists, then grazing cannot be a major control of phytoplankton population size. Thus, growth rates must be very low or some loss mechanism other than grazing must be important.

(4) Lake Ontario's secondary production should be determined empirically to allow comparison of zooplankton production and predation loss rates.

(5) Lake Ontario's major food web energy transfers appear to rely on heterotrophic pathways and the dynamics of detrital carbon. The role of detritus, heterotrophic bacteria, and the microbial foodweb in passing carbon to the traditional food web should be evaluated.

(6) Monitoring programs must be continued, expanded, and coordinated. Particular attention needs to be paid to lakewide shifts in indicator components of biological size spectra (as these are early signs of changes in ecosystem structure that may result from predation effects, particularly *Daphnia* size/species composition), spatial sampling densities required to characterize lakewide conditions and temporal sampling frequencies to establish trends, rate measures of fish growth and mortality, relative abundance, size, and condition of forage fishes, absolute biomass and production of dominant forage fishes (new technologies such as hydroacoustics should be considered), salmonine diet, systemwide physicochemical (including climatic) monitoring of the lake (interpretation of any changes in biological community structure must be made in the context of current environmental conditions), and standardization and calibration of methods (which is critical for multilake comparisons and ultimate interpretation of causality).

(7) Lake Ontario offers an excellent opportunity to apply an adaptive management approach to salmonine stocking. Salmonine stocking rates have been and are intended to be maintained at similar levels during the 1984–90 period. If, during that time, the forage base shows no apparent response to severe weather and/or predation, then a logical next step would involve increasing stocking rates. A stepped increase of 30–50% sustained for 4–6 yr would allow reasonable evaluation of the system response. Lacking substantial evidence of a collapse of the forage base or of food web enhancements on water quality (e.g. increased water clarity), the stocking rate could be incremented again until the system responded. The enhanced value of improved water quality and the expanded fishery should yield substantial social and economic benefits. It should also be noted that concern has been raised for the lack of alternative forage species in Lake Ontario, if the alewife population was decimated.

(8) A comprehensive understanding of trophic interactions and their spatial (e.g. inshore/offshore and warmwater/coolwater) and temporal (seasonal and diet) dynamics is needed. In 1986, the Board of Technical Experts (BOTE) of the Great Lakes Fishery Commission suggested an intensive lakewide effort modeled after the 1982 "Year of the Stomach" (i.e. a survey of stomach content) in the North Sea. This multinational initiative significantly advanced understanding of the North Sea food webs and improved the scientific basis for the management of multispecies fisheries. Equally important, it contributed substantial methodological advances which can now be applied elsewhere. The Council of Lake Committees accepted the BOTE recommendation and initiated a feasibility study. Workshop participants supported this feasibility study and rec-

ommended that agencies and universities support this effort. In addition, workshop participants encouraged development of mesoscale, whole-system experiments designed to evaluate responses of the Great Lakes communities to manipulations of food web interactions.

(9) Research is needed to determine the impact and implications (biological, social, and economic) of changes in food web dynamics and food web control on toxic substances cycling and contaminant bioaccumulation in fishes. Alewives are notoriously inefficient in food conversion and therefore are expected to pass a large amount of food through their gut and accumulate a commensurate amount of contaminants. Alewife are also high in oil content. A shift in salmonine diet toward other prey species, such as yellow perch and bloater chub, as predator–prey ratios change and predator control effects take place may result in lower contaminants in fish. These relationships need to be elucidated to enhance our understanding and management of this predator–prey system.

(10) Given the Lake Michigan experience, research is needed on the feasibility of experimentally stocking expatriated species (e.g. bloater chub) into Lake Ontario to achieve International Joint Commission and Great Lakes Fishery Commission goals of restoration and rehabilitation of native biological communities in the Great Lakes.

Synthesis and Concluding Remarks

There is an obvious need for a quantitative understanding of the trophic linkages operating within the Great Lakes ecosystem. Figure 1 presents a generalized model of a simple phytoplankton–zooplankton–planktivore–piscivore system and some possible outcomes due to trophic interactions. For example, intense stocking of piscivores can reduce planktivore biomass. Reduced planktivore biomass can result in an increase in zooplankton biomass which can in turn result in a decrease in phytoplankton biomass. This is precisely the cascading effect that was observed in Lake Michigan (Carpenter et al. 1985; Scavia et al. 1986; Kitchell and Carpenter 1987; Kitchell et al. 1988). Another possible scenario might be that intense fishing or predation (e.g. lamprey predation) might allow planktivore biomass to increase. The result would be a decrease in zooplankton biomass which could result in an increase in phytoplankton abundance. Elevated phosphorus loadings obviously increase in-lake phosphorus concentrations which can increase phytoplankton biomass (Vollenweider 1979). However, increased phytoplankton biomass does not necessarily increase zooplankton biomass (because of short algal life spans). Increased phytoplankton biomass may, in fact, have a direct impact on piscivores by lowered dissolved oxygen concentrations and loss of spawning habitat. These scenarios are but a few simple examples of interrelationships among ecosystem compartments. The need for a better understanding of food web interactions and how they are affected by physicochemical factors was one of the primary reasons for undertaking the Food Web workshops. Such understanding is fundamental to management of the Great Lakes ecosystem.

In general, nutrient and phytoplankton trend data are consistent with a nutrient control scenario for Lake Ontario phytoplankton, with light and nutrients (nitrogen during the 1970s and early 1980s and phosphorus thereafter) determining summer epilimnetic phytoplankton abundance. The shift to phosphorus limitation of phytoplankton growth has resulted in a decrease in blue-green algal abundance and a possible shift in size structure to smaller algae (Table 1). Rapidly increasing nitrogen/phosphorus ratios in Lake Ontario may soon evoke additional changes in phytoplankton species composition and biomass.

Salmon stocking in Lake Ontario has increased to the point where the total number stocked per unit area or unit volume is approximately 50% higher than in Lake Michigan (where food web effects have been manifest). Significant food web effects have not been broadly demonstrated in Lake Ontario. However, based on current stocking rates and some preliminary evidence (i.e. reduced slimy sculpin density, reduction in condition factor of adult chinook salmon, the decline of rainbow smelt populations in the Kingston basin), food web effects may become broadly manifest within the next few years. Monitoring the system must become a high priority, particularly tracking large *Daphnia* populations which are the key component of a suite of changes that should result if and as alewife stocks are reduced by piscivores. It was a consensus from workshop participants that to elucidate and understand the effects of nutrient controls (i.e. phosphorus abatement) and food web controls (i.e. predation) in Lake Ontario, water quality and fisheries agencies must (1) standardize monitoring techniques and establish and maintain compatible, long-term, limnological data sets, (2) cooperate on research (e.g. controlled, mesoscale, whole-system experiments) designed to quantify the rates (e.g. growth, predation, etc.) of food web interactions (emphasis must be placed on an interdisciplinary approach that explicitly accounts for time and spatial scale effects), and (3) promote initiatives which quantify the impact of changes in food web dynamics on reduction of toxic substance levels in Great Lakes fishes.

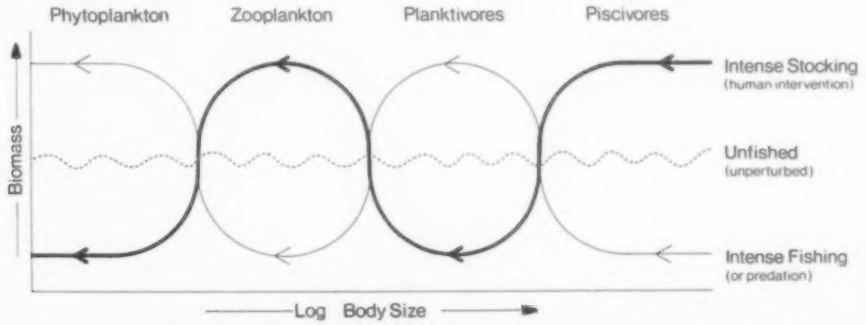


FIG. 1. Generalized model of a simple phytoplankton–zooplankton–planktivore–piscivore system and some possible outcomes due to interrelationships (adapted from Christie et al. 1987b).

As mentioned earlier, a fundamental management question is: "Are the Great Lakes phosphorus management and fishery management strategies compatible?" The phosphorus management strategy has been successful at reducing phosphorus loadings to the Great Lakes, while the fishery management strategy has been successful in establishing a high-value recreational fishery (Table 2). Water quality should continue to improve as phosphorus load reduction continues. Food web effects can be additive so that both the basic nutrient supply and the internal cycling of epilimnetic nutrients due to food web interactions can combine to enhance water clarity (Carpenter et al. 1985). However, phosphorus and fishery management strategies may in the long run promote ecosystem instability if they are not carefully coordinated. This concern arises because the alewife is now the crucial species for the support of a sustained sport fishery (alewife provide much of the diet of salmonines). Alewife can also control zooplankton and, secondarily, phytoplankton size spectra and species composition and can depress native forage stocks through competition and other ecological interactions. By decreasing phosphorus loadings and increasing salmonine predation pressure, we may be putting simultaneous negative feedback pressures on alewife. Another important factor in alewife mortality may be winter severity, which may periodically overwhelm density-dependent controls. How much stocking and phosphorus control is too much? This depends on the relative priorities of management goals (i.e. maximizing fish production, maximizing water clarity, restoring native species, etc.).

Coordination among agencies is now more important than ever before. The International Joint Commission and the Great Lakes Fishery Commission have many goals in common but some may come into conflict as a result of fisheries management practices which can affect food web interactions that are expressed in both water quality and contaminant concentrations. One way of helping to ensure compatibility of phosphorus and fishery management strategies would be for the International Joint Commission and Great Lakes Fishery commission to sponsor workshops on the status of Lake Ontario every 3–5 yr to evaluate trends, review progress toward management goals, explicitly account for interrelationships between management programs, and provide opportunity for midcourse corrections.

The lessons of Lake Michigan's recent history and the opportunities of Lake Ontario's future offer unique potential for a marriage between basic research and applied scientific management. We should nurture this union and test it. If we are wrong about the role of food web dynamics in enhancing water clarity, we have lost little, for we will have gained knowledge through basic science. If we are right, then we will have gained both the basic understanding and the success of its application.

Acknowledgements

We express our sincere thanks to all workshop participants. Without their contributions and involvement, this manuscript would not be possible. In addition, we thank members of the workshop steering committee (D. M. Whittle, T. B. Reynoldson, and C. J. Edwards) for their enthusiasm and support. Financial support for the Food Web workshops was provided by the Science Advisory Board of the International Joint Commission.

References

BRANDT, S. B. 1986. Food of trout and salmon in Lake Ontario. J. Great Lakes Res. 12: 200–205.

BRANDT, S. B., D. M. MASON, D. B. MACNEILL, T. COATES, AND J. G. GANNON. 1987. Predation by alewives on larvae of yellow perch in Lake Ontario. Trans. Am. Fish. Soc. 116: 641–645.

CARPENTER, S. R., J. F. KITCHELL, AND J. R. HODGSON. 1985. Cascading trophic interactions and lake productivity. BioScience 35: 634–639.

CHRISTIE, W. J., K. A. SCOTT, P. G. SLY, AND R. H. STRUS. 1987a. Recent changes in the aquatic food web of eastern Lake Ontario. Can. J. Fish. Aquat. Sci. 44(Suppl. 2): 37–52.

CHRISTIE, W. J., G. R. SPANGLER, K. H. LOFTUS, W. A. HARTMAN, P. J. COLBY, M. A. ROSS, AND D. R. TALHELM. 1987b. A perspective on Great Lakes fish community rehabilitation. Can. J. Fish. Aquat. Sci. 44(Suppl. 2): 486–499.

HARTIG, J. H., AND J. E. GANNON. 1986. Opposing phosphorus and nitrogen trends in the Great Lakes. Alternatives 13: 19–23.

INTERNATIONAL JOINT COMMISSION (IJC). 1986. Third biennial report under the Great Lakes Water Quality Agreement of 1978 to the governments of the United States and Canada and the States and Provinces of the Great Lakes Basin. IJC, Washington, DC, and Ottawa, Ont., Canada.

1987a. Rehabilitation of Lake Ontario: the role of nutrient reduction and food web dynamics (based on conclusions and recommendations of Food Web II Workshop). IJC, Windsor, Ont., Canada.

1987b. Report on Great Lakes water quality. Great Lakes Water Quality Board, Windsor, Ont., Canada.

KITCHELL, J. F., AND S. R. CARPENTER. 1987. Piscivores, planktivores, fossils and phorbins, p. 132–146. *In* W. C. Kerfoot and A. Sih [ed.] Predation: direct and indirect impacts on aquatic communities. University Press New England, Hanover, NH.

KITCHELL, J. F., AND L. B. CROWDER. 1986. Predator–prey interactions in Lake Michigan: model predictions and recent dynamics. Environ. Biol. Fishes 16: 205–211.

KITCHELL, J. F., M. S. EVANS, D. SCAVIA, AND L. B. CROWDER. 1988. Food web regulation of water quality in Lake Michigan. J. Great Lakes Res. 14: 109–114.

LEHMAN, J. T. 1988. Algal biomass unaltered by food web changes in Lake Michigan. Nature (Lond.) 332: 537–538.

MINNS, C. K., E. S. MILLARD, J. M. COOLEY, M. G. JOHNSON, D. A. HURLEY, K. H. NICHOLLS, G. W. ROBINSON, G. E. OWEN, AND A. CROWDER. Production and biomass size spectra in the Bay of Quinte, a eutrophic ecosystem. Can. J. Fish. Aquat. Sci. 44: 148–155.

O'GORMAN, R., R. A. BERGSTEDT, AND T. H. ECKERT. 1987. Prey fish dynamics and salmonine predator growth in Lake Ontario, 1978–84. Can. J. Fish. Aquat. Sci. 44(Suppl. 2): 390–403.

SCAVIA, D. 1979. Examination of phosphorus cycling and control of phytoplankton abundances in Lake Ontario with an ecological model. J. Fish. Res. Board Can. 36: 1336–1346.

1980. An ecological model of Lake Ontario. Ecol. Model. 8: 49–78.

SCAVIA, D., AND G. L. FAHNENSTIEL. 1987. Dynamics of Lake Michigan phytoplankton: mechanisms controlling epilimnetic communities. J. Great Lakes Res. 13: 103–120.

SCAVIA, D., G. L. FAHNENSTIEL, M. S. EVANS, D. J. JUDE, AND J. T. LEHMAN. 1986. Influence of salmonine predation and weather on long-term water quality trends in Lake Michigan. Can. J. Fish. Aquat. Sci. 43: 435–443.

SMITH, V. H. 1983. Low nitrogen to phosphorus ratios favor dominance by blue-green algae in lake phytoplankton. Science (Wash., DC) 221: 669–671.

STEVENS, R. J. J., AND M. A. NEILSON. 1987. Response of Lake Ontario to reductions in phosphorus load, 1967–82. Can. J. Fish. Aquat. Sci. 44: 2059–2068.

TALHELM, D. R. 1987. Economics of Great Lakes fish: 1985 assessment. Technical report. Great Lakes Fishery Commission, Ann Arbor, MI.

TAYLOR, W. D., H-J. FRICKER, AND D. R. S. LEAN. 1987. Zooplankton seasonal succession in Lake Ontario at northshore, midlake, and southshore stations in 1982, and a comparison with 1970. Can. J. Fish. Aquat. Sci. 44: 2178–2184.

THOMANN, R. V., D. M. DITORO, R. P. WINFIELD, AND D. J. O'CONNOR. 1975. Mathematical modeling of phytoplankton in Lake Ontario. Part 1: Model development and verification. Ecol. Res. Ser. EPA-660/375005. U.S. EPA, Corvalis, OR.

VOLLENWEIDER, R. A. 1979. Das Nährstoffbelastungskonzept als Grundlage für den externen Eingriff in den Eutrophierungsprozess stehender Gewässer und Talsperren. Z. Wassar- Abwasser-Forsch. 12: 46–56.

Coastal Wetlands of Three Canadian Great Lakes: Inventory, Current Conservation Initiatives, and Patterns of Variation

P. G. R. Smith

Ontario Ministry of Natural Resources, 820 Yonge Street, R.R. 2, Aurora, Ont. L4G 3G8, Canada

V. Glooschenko

Ontario Ministry of Natural Resources, Toronto, Ont. M7A 1W3, Canada

and D. A. Hagen

Ontario Ministry of Natural Resources, Toronto, Ont. M7A 1W3, Canada

Smith, P. G. R., V. Glooschenko, and D. A. Hagen. 1991. Coastal wetlands of three Canadian Great Lakes: inventory, current conservation initiatives, and patterns of variation. Can. J. Fish. Aquat. Sci. 48: 1581–1594.

The decline of wetlands, including those in the Great Lakes coastal zone, prompted the Government of Ontario to initiate steps towards a wetland management policy in 1981. Wetland inventory and evaluation in southern Ontario began in 1983. To date, 1982 wetlands have been evaluated totalling 390 000 ha. These include 160 coastal wetlands, 64 of these on Lake Ontario and the remainder on the other Great Lakes and connecting channels. Current wetland conservation initiatives are outlined including the Wetlands Planning Policy Statement and Conservation Lands Act. Although the values of Ontario's coastal wetland areas are increasingly being recognized, there has been no comprehensive study to show patterns in coastal wetland ecology. Aided by analysis of variance, ordination, and cluster analysis, we show patterns of variation in wetland and site types, soils, dissolved solids, vegetation complexity, and rare flora and fauna which differ between wetlands along Lakes Ontario, Huron, Erie, St. Clair, and connecting channels. Wetlands of Lake Huron reflect a more northern species composition, less organic soil, and more swamp and fen habitat. Along Lakes Erie, Ontario, and St. Clair the predominant marshes have smaller swamp components, organic soils, and considerable dissolved solids.

L'assèchement des terres marécageuses, y compris celles de la zone côtière des Grands Lacs, a incité le gouvernement de l'Ontario à prendre des mesures en vue de l'établissement d'une politique de gestion des terres marécageuses en 1981. L'inventaire et l'évaluation des terres marécageuses du sud de l'Ontario a commencé en 1983. Jusqu'à maintenant, 1 982 terres marécageuses totalisant 390 000 ha ont été évaluées. Elles comprennent 160 terres marécageuses côtières : 64 bordent le lac Ontario et le reste, les autres Grands Lacs et les chenaux de navigation. Les grandes lignes de initiatives courantes pour la protection des terres marécageuses sont présentées, y compris la Déclaration de principes sur la planification de la gestion des terres marécageuses et la Loi sur la protection des terres. Même si la valeur des terres marécageuses côtières de l'Ontario est de plus en plus reconnue, aucune étude détaillée visant à établir les régimes écologiques des terres marécageuses côtières n'a été réalisée. À l'aide d'analyses de la variance, de grappes et d'ordination, on établit des régimes de variation pour ce qui et des types de terres marécageuses et de sites, des sols, deds solides dissous, de la diversité des végétaux ainsi que des espèces rares de faune et de flore qui varient selon les terres marécageuses des lacs Ontario, Huron, Érié et Sainte-Clair et des chenaux de navigation. Les terres maréageuses du lac Huron sont peuplées d'espèces caractéristiques des zones boréales, contiennent moins de sol humifère, mais englobent plus de marécages et de tourbières minérotrophes. Dans le cas des lacs Érié, Ontario et Sainte-Clair, les principaux marais englobent moins de marécages, contiennent moins de sols humifères, mais plus de solides dissous.

Received February 6, 1989
Accepted October 26, 1990
(JA038)

Reçu le 6 février 1989
Accepté le 26 octobre 1990

Wetland loss and degradation, particularly along the Great Lakes, has been of much concern to planners, resource managers, and the general public in both Canada and the United States (Francis et al. 1979; Herdendorf et al. 1986; Herdendorf 1987). Yet many coastal wetlands have not received sufficient protection to maintain their essential ecological functions for the future (Smith 1987).

Wetland loss on the Canadian side has been documented by a number of studies. Reid (1981) and Bardecki (1981) have commented on various aspects of wetland loss. Snell (1982, 1987) has estimated that over 1.4 million ha (61%) of southern Ontario's original wetlands have been converted since settlement times. McCullough (1981) described the loss of waterfowl habitat on Lakes Ontario and St. Clair. Change in habitat loss in the wetland area of western Lake Ontario was noted by Whillans (1982), and Lemay and Mulamoottil (1984) documented changing land uses in Lake Ontario waterfront marshes.

This paper seeks first to provide an overview of Ontario government initiatives on wetlands, particularly Great Lakes' coastal wetlands. In addition, the paper summarizes ecological knowledge of coastal wetlands on the Canadian side of the lakes based on recent inventories undertaken as part of the govern-

ment's wetland program. Graphical and statistical methods are used in these analyses.

Coastal Wetland Values

A review of the values of coastal wetlands was provided by Herdendorf et al. (1986). Some of the greatest values for coastal wetlands lie in their habitat potential for migratory birds and waterfowl. For Lake Ontario, Dennis and Chandler (1974), Dennis et al. (1984), and Crowder and Bristow (1988) have documented the utility of wetlands with regard to waterfowl. Their value for fish habitat is also well recognized. Stephenson (1988, 1989) has recently documented fish use of coastal marshes for various aspects of reproduction throughout the year (spawning, nursery). In addition, Herdendorf (1987) has noted that these coastal wetlands are important because of the cover they provide for juvenile and forage fish. Approximately 43 species of fish are or once were associated with the coastal marshes of western Lake Erie. Often as much as 90% of the standing fish crop in wetlands consists of forage species.

Wetland Inventory and Evaluation

The decline of wetland resources in Ontario prompted the Government of Ontario to initiate steps towards a wetlands management policy in 1981. The first major components of this initiative centred on a cooperative federal–provincial mapping inventory of the wetland resource and on development of an inventory and evaluation system. The mapping was completed by Environment Canada for all of southern Ontario (Snell 1987).

Development of a wetland inventory and evaluation system was initiated in 1981 by the Wildlife Branch of the Ontario Ministry of Natural Resources (OMNR) and Lands Directorate/ Canadian Wildlife Service of Environment Canada. This document drew from many sources, including a wetland evaluation model proposed by the Federation of Ontario Naturalists (Reid et al. (1980) as discussed by Patterson (1984). From 1981 to 1983, preliminary versions of the Ontario Wetland Evaluation System were tested and modified. Glooschenko (1983) has discussed the evolution of this evaluation system. The current version (Environment Canada and the OMNR 1984) has been in use for five complete field seasons.

The primary goal of wetland inventory and evaluation is to rank wetlands for the purposes of setting planning and management priorities. Such ranking is a planning tool that can be incorporated into government policy to facilitate informed land-use decisions.

Wetland inventory and evaluation includes field reconnaissance inventory of each wetland. This includes the identification and mapping of vegetation communities, summary of existing knowledge about rare species, and measurement of other variables such as exposure to wave action.

When complete, these field data are coupled with knowledge of local biologists and naturalists and translated into evaluation scores using formulae laid out in the wetland manual. These scores are then used to rank the wetlands into seven different classes, class 1 being the highest or most valuable and class 7 being the lowest ranked.

Both the inventory and evaluation deal with biological, social, hydrological, and special feature information. In the scoring scheme, each of these four components has a maximum score of 250 points. Each component is weighted equally in determining the final ranking of a wetland.

Ontario's provincial wetland guidelines give priority for protection to provincially significant wetlands (classes 1 and 2) as specified in OMNR's (1984) wetland guidelines and to those additional wetlands (classes 3–7) identified by municipalities as significant and addressed within their planning documents.

Inventory and Evaluation Results

A program of wetland inventory evaluation began in 1983 and to date, 1982 wetlands have been evaluated, totalling 390 000 ha. A large portion of southern Ontario's wetlands have now been evaluated and this includes 160 coastal wetlands and wetland complexes, 64 of these on Lake Ontario and the remainder on the other Great Lakes and connecting channels.

Although the values of Canadian coastal wetland areas are increasingly being recognized, there has been no comprehensive study to show ecological relationshps within the coastal wetlands. An earlier paper (Glooschenko 1985) compared some Great Lakes coastal wetlands with inland wetlands that were assessed by OMNR. The present paper describes patterns of variation in wetland and site types, soils, vegetation complexity, and rare and significant flora and fauna which differ significantly between wetlands in the different geographic areas. The features of 64 Lake Ontario coastal wetlands are treated in some detail, including characterization of their variation in relation to coastal geomorphology.

Conservation Initiatives

In the past several years, there have been a number of provincial initiatives to conserve and manage wetlands as well as one to provide coordinated management of the shorelines of the Great Lakes.

In December 1986, OMNR initiated a provincial shoreline management program. The goal of the program was to minimize danger to life and property damage from flooding, erosion, and other similar hazards along shorelines and to ensure that shoreline development adequately addresses flooding and erosion hazards through both public and private management and development alternatives (OMNR 1987). Guidelines distributed in 1987 identify the preservation, protection, emergency response, public information, environment, and monitoring components of Shoreline Management Plans.

Recent wetland policy and program initiatives include the release of a new Draft Wetlands Planning Policy Statement under the Planning Act and the announcement of the Conservation Lands Tax Reduction Program. Both are discussed below.

Wetlands Planning Policy Statement

The 1983 Planning Act states that the "protection of the natural environment" and "features of significant natural ... interest" are "matters of provincial interest."

The Planning Act is the primary piece of legislation governing municipal planning in Ontario. Under section three of the Act, the Province is able to articulate land use interests in the form of policy statements. These policy statements are released first in draft for public review and comment and then formally approved under the Planning Act. Once approved, all municipalities, provincial government ministries, agencies, boards, and commissions are required to have regard to the provisions of those policy statements.

The provincial government has had a long-standing commitment to the protection of wetlands, and in November 1988 it released a Draft Wetlands Planning Policy Statement for public review and comment. The proposed Wetlands Planning Policy Statement will not, by itself, ensure wetland protection. It is one element of a comprehensive wetland management program administered by OMNR.

The proposed Wetlands Planning Policy Statement contains policies to identify and protect provincially significant class 1 and 2 wetlands. Regional and local municipalities may apply the provisions of the policy statement for those wetlands within their planning jurisdiction which are deemed to be regional or local in significance.

The proposed policy statement applies province-wide, even though the evaluation system on which wetlands are classified applies only to those wetlands located south of the Precambrian Shield. OMNR has also initiated the development of an evaluation system for northern Ontario, but until this latter system is in place, wetland values in Ontario are defined in consultation with OMNR as those which (i) provide habitats required for the maintenance of healthy fish or wildlife populations of importance to achieving provincial management objectives, and/or (ii) have an essential hydrological role in the watershed where they exist, and/or (iii) have a significant social or economic benefit.

The draft policy is based on the following principles:

(1) Wetlands are essential natural resources and the Province is committed to their protection.

(2) There will continue to be demands on wetlands for conversion to other land uses. Some of these demands may have to be accommodated, and for this reason the policy statement establishes criteria by which the need for locating land uses in and adjacent to wetlands can be fully evaluated.

(3) All planning authorities in Ontario will share in the responsibility for protection of wetlands.

The draft policy states that all municipalities, planning boards, and resource management agencies should identify and protect provincially significant class 1 and 2 wetlands within their jurisdictions in the context of local, regional, and provincial land use planning objectives. Class 3–7 wetlands may also be identified in planning documents and protected in a manner deemed appropriate by municipal authorities.

New land uses permitted on, or adjacent to, a provincially significant wetland should be compatible with the wetland so that the wetland values are maintained or improved, as defined by the evaluation system. In northern Ontario, above the Precambrian Shield where the evaluation system does not apply, changes in wetland values will be assessed by OMNR on a site-specific basis.

Wetlands are also to be placed in a restrictive zoning category which permits only natural features and land uses compatible with wetland maintenance. In consideration of any such proposals, the criteria for land-use compatibility should take into account that total evaluation score and classification of each wetland be maintained or improved.

If land-use change is justified in accordance with the above, the development should be carried out in a manner to minimize its negative impact on the affected wetland.

To aid in implementation, OMNR will (i) inform landowners and the general public on the value of wetlands and provide information on wetland management, as well as maps and other technical information, (ii) make a presentation or provide technical expertise to the Ontario Municipal Board or other appeal body where a matter related to this planning policy may be at issue, and (iii) issue the associated Implementation Guidelines for the Wetlands Policy Planning Statement and jointly administer the policy statement with the Ontario Ministry of Municipal Affairs (OMMA).

The mandate of OMMA includes the administration of the Planning Act. It is responsible for the review and/or approval of various municipal land-use planning documents and for ensuring that municipalities and planning authorities have had regard for the Wetlands Planning Policy Statement. OMNR and OMMA are jointly responsible for the administration of the Wetlands Planning Policy Statement.

Conservation Lands Tax Reduction Program

The Conservation Lands Tax Reduction Program provides up to 100% tax rebate to landowners of class 1–3 wetlands as well as certain other heritage lands. The tax reduction program, provided under the Conservation Lands Act, is an incentive for private landowners to maintain in a natural state those lands which contribute to Ontario's conservation and heritage objectives. To be eligible, landowners must agree to maintain the land for the long term and not to conduct activities which would have a negative impact on its values.

Evaluation and Inventory of Great Lakes Coastal Wetlands

Methods of Analysis

In the following section of the paper, we analyze the data collected on each of the 160 coastal wetlands evaluated by OMNR (Fig. 1). The intent is to (1) describe the diversity of wetland types along the Great Lakes and their connecting channels, (2) investigate factors that contribute to patterns of variation, and (3) develop empirical classifications of the types of coastal wetlands.

Methods of analysis used include analysis of variance, both parametric and nonparametric, cross-tabulation, ordination, and cluster analysis. Where numeric variables conformed to the assumptions of a normal distribution and homogeneity of variances, parametric analyses of variance were performed. In some cases, logarithmic and arcsine transformations were used to normalize distributions and stabilize variances (Steele and Torrie 1980). In other cases, the Kruskal–Wallis nonparametric test was used. An ordination using principal components analysis revealed the primary gradients of wetland variation. Centred, standardized principal components analysis with varimax rotation was the ordination technique used (Pielou 1984). Other ordination techniques, such as detrended correspondence analysis and multidimensional scaling, are also popular in such ecological analyses (Gauch 1982; Pielou 1984). Cluster analysis indicated the general categories of wetlands based on their physical structure and vegetation composition. Ward's minimum variance clustering method was employed (Gauch 1982; Pielou 1984).

Variables used in the analyses include numeric variables measuring the wetlands' site type (lacustrine, riverine, etc.), wetland type (marsh, swamp, etc.), soil type, nutrient status, and vegetation complexity (see Environment Canada and OMNR (1984) for definitions and detailed descriptions of these variables). A number of categorical variables classifying the wetlands' vegetation interspersion, open-water configuration, and exposure to wave action were also analyzed. In multivariate

FIG. 1. Location of coastal wetlands (triangles) of the Great Lakes and connecting channels evaluated by OMNR. Note that one triangle may represent more than one wetland or wetland complex.

analyses, these categorical variables were included as "dummy" variables (i.e. either 0 or 1 for each category; see Draper and Smith 1984). Similarly, the dominant plant taxa of each wetland's vegetation communities were recorded as present or absent (i.e. 1 or 0).

The species composition of wetland vegetation communities is not emphasized in the wetland evaluation system. Rather the structural or physiognomic composition is the major focus. Thus, only dominant species can be used in the analysis presented here. Because OMNR wetland assessments are based on reconnaissance inventory rather than detailed inventory, a number of species were lumped into genera or family groups (e.g. Poaceae, Cyperaceae, *Acer*). A sample of 80 wetlands was used in multivariate analyses, as these have consistent and comparable data on dominant species composition.

Results and Discussion

The inventories and evaluations of wetlands undertaken by OMNR include 160 wetlands along the Great Lakes and their connecting channels with a total area of almost 40 000 ha (Fig. 1 and 2). Virtually all of these are south of the Precambrian Shield and lie along Lakes Ontario, Erie, St. Clair, and Huron, Georgian Bay, and the St. Lawrence, Niagara, Detroit, and St. Clair rivers. Seven wetlands along the northwestern coastline of Lake Superior were evaluated by the Lakehead Region Conservation Authority but were not included in analyses because of differences in methods.

Most wetlands along the Great Lakes and connecting channels score highly and are ranked in the higher classes of 1–3 (Fig. 2). They score particularly highly in the special features and social components of the evaluation system. Hydrological scores are lower than inland wetlands (Collins and Maltby 1984; Glooschenko 1985).

General Characteristics of the Wetlands of Each Lake and Connecting Channel

St. Lawrence River

Along the St. Lawrence River, 3500 ha of wetland habitat at 27 sites have been assessed by OMNR (Fig. 1 and 2). These primarily are wetlands along river shores and at the mouths of smaller rivers which enter the St. Lawrence. Marsh is the predominant wetland type. A variety of physiographic environments surround the St. Lawrence River between Lake Ontario and the Quebec border. The Frontenac Axis, a southern extension of the Precambrian Shield, with its low, rounded hills, forms the Thousand Islands. Farther downstream, limestone plain, till plain, and riverine deposits are characteristic (Chapman and Putnam 1984). Environment Canada (1985) described

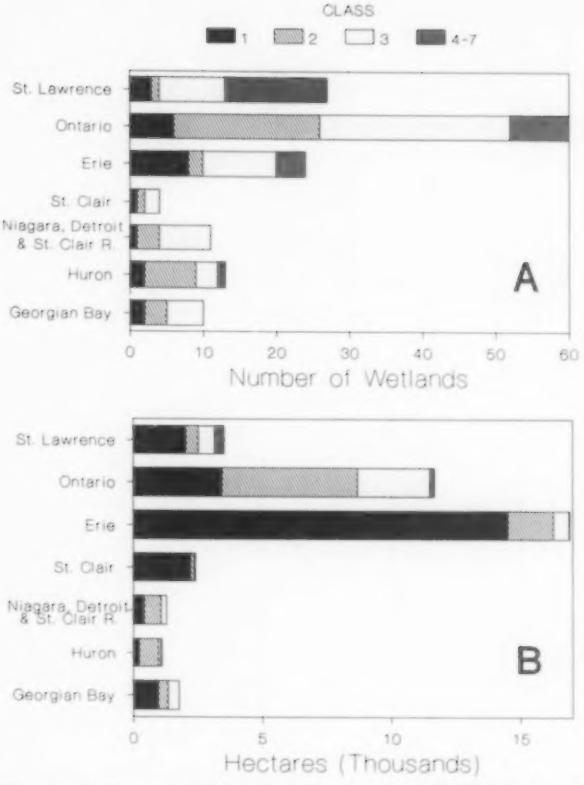


FIG. 2. (A) Numbers and (B) hectares of coastal wetlands evaluated along the Great Lakes and connecting channels. Numbers and hectarage in each class are shown.

St. Lawrence River wetlands between Cornwall and the Gulf of St. Lawrence. Species composition appeared quite similar to the lower St. Lawrence wetlands described here, except that *Typha* appeared to be a less dominant genus upstream. That study typified the wetlands as occurring in areas of weak current, shallow bays and on deposits of clay and gravel. Auclair et al. (1976) studied the interrelationships between environmental parameters and plant community productivity and structure in emergent *Scirpus–Equisetum* stands in the Lake St. Francis portion of the river. Tidal freshwater and brackish water marshes with dominants such as *Spartina* characterize St. Lawrence River wetlands in Quebec nearer the Gulf of St. Lawrence (Lacoursiere 1969).

Lake Ontario

Lake Ontario's 64 wetlands totalling almost 12 000 ha are scattered along the shores in river mouths and embayments and behind bars and barriers (Fig. 1, 2, and 3). These wetlands dot the entire length of the lake, but the largest portion of the wetland area is concentrated east of Presqu'ile Provincial Park.

The coastal geomorphology of Lake Ontario coast has determined the form of the wetlands. East of Presqu'ile is a limestone plain from which glaciers stripped most of the overburden (Chapman and Putnam 1984). Along the shores of the Bay of Quinte, particularly on the southern shore, deeper clay sediments are present. The large Sawguin Creek and Big Island Marshes lie here. Crowder et al. (1986) described in some detail

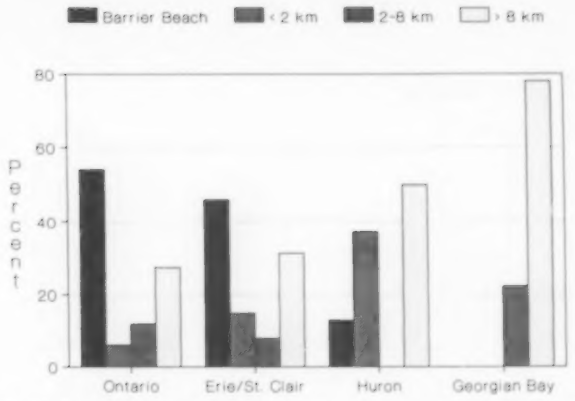


FIG. 3. Presence of barrier beaches and fetch distances for Great Lakes coastal wetlands. Percentages are significantly different between the water bodies (chi-square, $P < 0.05$).

the wetlands and fauna of the Bay of Quinte. The southern and eastern sides of Prince Edward County have irregular coastlines where deep valleys dissect the shoreline and form long deep bays that are often closed by baymouth bars (Chapman and Putnam 1984; Whitcomb et al. 1973). Such sites possess large wetlands such as those at Weller's Bay, West Lake, Pleasant Bay, and Big Sandy Bay.

The shores of the western end of Lake Ontario are composed of a variety of glacial tills and lacustrine deposits overlying several different types of bedrock. The surficial material dates from previous postglacial lakes, particularly Lake Iroquois. In a number of areas, these deposits are actively eroding and form bluffs, most notably at the Scarborough Bluffs. In yet other areas, river valleys, cut during prehistoric times of lower water levels, are "drowned" by present lake levels. Many wetlands form in these locations, notably in the Niagara Peninsula. These sites include Jordan Harbour and Martindale Pond as well as the mouths of 15, 16, and 17 Mile creeks. T. Whillans, R. Smardon, and W. Busch (unpubl. data) noted that the waterfront wetlands of western Lake Ontario generally have high macrophyte productivity and interspersion of vegetation types.

Lake Ontario's wetlands are, on average 80% marsh and 20% swamp. Bog habitat occurs at Nut Island Duck Club Marsh on Amherst Island and Big Sandy Bay on Wolfe Island; a fenlike "panne" habitat occurs at Presqu'ile Provincial Park. Fifty-five percent of Lake Ontario's total wetlands lie behind barrier beaches (Fig. 3). Twenty-nine percent of the wetland (area) is in a riverine location, 27% is on protected bays, another 25% is in river mouth locations, 17% is exposed to the lake proper, and less than 2% is palustrine (Fig. 4).

Thirty-three different provincially significant bird species, as designated by the wetland evaluation system (see Environment Canada and Ontario Ministry of Natural Resources 1984), occur in Lake Ontario's coastal wetlands. The six most frequent species are shown in Fig. 5. Some of these species demonstrate affinities for the Great Lakes shorelines as discussed earlier (also see Glooschenko et al. 1988a). Others like the northern harrier have no particular affinity for coastal wetlands.

Nineteen different plant species in Lake Ontario's coastal wetlands are considered provincially rare by Argus et al. (1982–88). Two species are found primarily in the eastern end of Lake Ontario. *Alisma gramineum* occurs, and indeed is sometimes

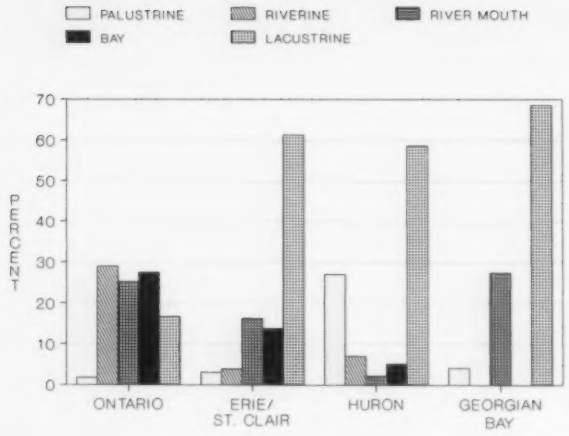


FIG. 4. Percentage of wetland area in the different site types for the Great Lakes.

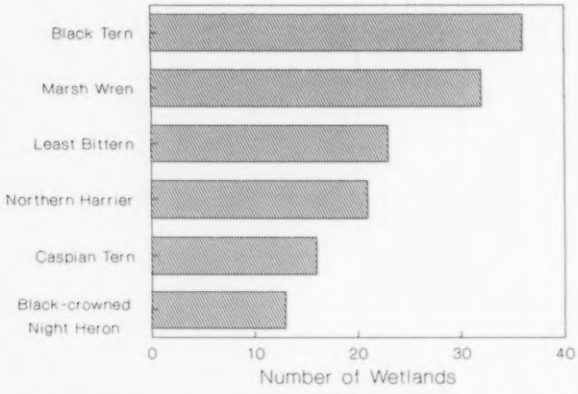


FIG. 5. Number of Lake Ontario wetlands in which the six most frequent provincially significant birds species occur: black tern (*Chlidonias niger*), marsh wren (*Cistothorus palustris*), least bittern (*Oxobrychus exilis*), northern harrier (*Circus cyaneus*), Caspian tern (*Sterna caspia*), and black-crowned night heron (*Nycticorax nycticorax*).

very abundant, in nine wetlands east of Presqu'ile Provincial Park, particuarly those on Wolfe Island. *Alisma gramineum* is widely distributed in western North America, but in the eastern part of the continent is restricted to the St. Lawrence Valley and eastern Lake Ontario. In four wetlands in Prince Edward County and on Wolfe Island, *Peltandra virginica* is present. *Peltandra virginica* is also widely distributed in the eastern and southern United States but is found only at a few widely scattered localities in Ontario.

Lake Erie

The 28 Lake Erie coastal wetlands and wetland complexes occupy almost 17 000 ha (Fig. 1 and 2), two thirds of which are contained in the Long Point wetland complex which includes Long Point proper, Big Creek, Turkey Point, and wetlands lining Long Point Bay. Other large wetlands exist west of Long Point. Some of these are the swamps and marshes of Rondeau Bay, major wetlands at the mouths of Cedar and Big creeks in Essex County, and, of course, Point Pelee (Herdendorf 1987). Smaller wetlands are scattered along the shorelines east of Long Point primarily at rivermouths. Large, lake-influenced wetlands occur up the mouth of the Grand River near the eastern end of Lake Erie. Clay and sand plains border the Lake Erie shoreline.

Niagara, Detroit, and St. Clair rivers

Seven wetlands totalling over 1200 ha occur along the Detroit River, particularly near its mouth (Herdendorf 1987), where thousands of waterfowl stage during migration periods (Dennis et al. 1984). Wetlands assessed on the connecting channels include one on the Niagara River and three on the St. Clair River (Fig. 1 and 2).

Lake St. Clair

Lake St. Clair is well-known for its extensive and important wetlands (McCullough 1981, 1985; Herdendorf et al. 1986). Four wetlands totalling over 2400 ha have been evaluated by OMNR (Fig. 1). These lie along the eastern shore, at the mouth of the Thames River, and at two sites along the south shore. The particularly large (over 10 000 ha) Walpole Island marshes have not yet been evaluated using OMNR wetland methods, as they lie outside provincial jurisdiction. Walpole and other islands form the massive delta of the St. Clair River, a classic example of a bird's foot digitate delta (Bird 1984).

Lake Huron

Lake Huron has 13 wetlands consisting of 1300 ha (Fig. 1 and 2). The coastline has few natural barriers, estuaries, or drowned river valleys and portions are highly developed for recreational use. Considerable diversity in coast type exists. From Sarnia to Point Edward, sandy beaches prevail with some lagoon wetlands (Chapman and Putnam 1984). Kettle Point, a bedrock shelf, juts out into the lake and provides a sheltered site for another wetland. The meanders of the Ausable River transect the dune system at Pinery and Ipperwash; between the dunes lie the large Port Franks interdunal forested swamps and wet meadows. From Grand Bend to Port Elgin, a shorecliff of 15–30 m in height defines the shoreline and precludes wetland development. On the Bruce Peninsula, where the shore is primarily dolostone bedrock, a more complex coastline has developed. Wetlands are more numerous and include shoreline fens, such as that at Dorcas Bay, generally uncommon elsewhere on the Great Lakes shores. A number of these wetlands were also analyzed in detail by Charlton (1986; also Charlton and Hilts 1989) in his study of fens, marshes, and bogs in the Bruce Peninsula. A number of wetlands along the coast of Manitoulin Island were discussed by Smith (1987). The attributes of some coastal marshes in Bruce County were described by Fahselt and Maun (1980).

Georgian Bay (Lake Huron)

Only the portion of Georgian Bay southwest of the Precambrian Shield has been surveyed by OMNR for wetlands. A total of 1829 ha in 10 wetlands have been evaluated to date (Fig. 1 and 2). The rugged shoreline of the eastern side of the Bruce Peninsula prevents the development of extensive wetlands. One exception is Wingfield Basin, a small, sheltered cove at the base of the Niagara Escarpment at Cabot Head. The long, often sandy shoreline of Nottawasaga Bay also lacks wetlands, except in interdunal areas, the few harbours, and rivermouths. Southeastern Georgian Bay, while rocky, includes some sheltered embayments where a number of shoreline marshes have developed. Noteworthy amongst these are the marshes of Matchedash Bay.

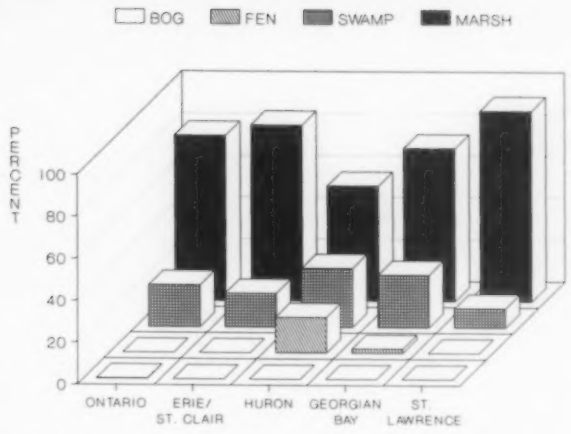


FIG. 6. Wetland types for coastal wetlands on the Great Lakes and St. Lawrence River. Percentage of marsh, swamp, and fen is significantly different between lakes (for statistic and P values, see Table 1).

Patterns of Variation

Wetland type

Overall, the dominant wetland type in southern Ontario is forest swamp (Glooschenko et al. 1987). In contrast, Ontario's Great Lakes coastal wetlands, like those on the American side, are predominantly marsh (Fig. 6; also see Herdendorf et al. 1981; Glooschenko 1985; Herdendorf et al. 1986; Herdendorf 1987). The classic pattern described by many authors is a band of submerged plants farthest lakeward, emergents somewhat closer to shore, and a zone of shrub and forest swamp in the backshore area. This gradient of water depth is one of the major gradients influencing the structure and composition of shoreline wetlands (Hutchinson 1975; Day et al. 1988). The well-known fluctuations of water levels in the Great Lakes contribute to this preponderance of marsh and to the diversity of vegetation by contributing to natural disturbance (Keddy and Reznicek 1986). Disturbance gradients are another key determinant of wetland vegetation (Day et al. 1988).

Predominance of marsh, however, is not uniform along the lakes. Lake Huron wetlands, particularly those along the western side of the Bruce Peninsula, have a higher percentage of fen and swamp habitat and less marsh (Fig. 6; Table 1). Most fen habitat develops in areas with calcareous bedrock such as the Bruce Peninsula (Reddoch 1982; Charlton 1986; Charlton and Hilts 1989). The percentage of wetlands on a protected bay, presence of a barrier beach, and fetch distance (Table 1; Fig. 3 and 4) are all measures of level of disturbance due to wave and storm action. Swamp habitat in Great Lakes wetlands is positively associated with wetland location on protected bays (F-test, $P < 0.05$).

Soil composition and productivity

Soil composition in wetlands varies significantly among the lakes (Table 1; Kruskal–Wallis test, $P < 0.01$; soil composition determined from the soil maps). The soils of the wetlands of Lakes Ontario, Erie, and St. Clair contain a significant percentage of organics (Fig. 7). Soils on Lake Huron consist of a lower percentage of organics. Georgian Bay wetlands are almost entirely underlain by mineral soils (Fig. 7; Table 1). This reflects a north–south productivity gradient as well as differences in substrate and physiographic location. The north–south productivity gradient is reflected in the significant difference in levels of total dissolved solids among the lakes (Table 1). Levels are lower in northern wetlands of Lake Huron, Georgian Bay, and the St. Lawrence River than in those of the more southern lakes.

Coastal geomorphology

Barrier beaches are prevalent on Lakes Erie and Ontario, particularly the latter (Fig. 3). The genesis of these landforms often dates to previous postglacial lakes that had higher water levels. Drowned river valleys, artifacts of previous postglacial lakes, also provide a sheltered environment in which organic soil can accumulate. These are notable features along Lake Ontario, especially in the Niagara region and along the northwest shore. Almost 28% of wetlands occur in the numerous sheltered bays along Lakes Erie and Ontario, particularly eastern Lake Ontario (Fig. 4). All these protected locations would promote the formation of organic soils because of little wave action.

In contrast, the wetlands of Lake Huron and especially Georgian Bay are primarily lacustrine wetlands (Fig. 4) exposed to some wave action and storm events. This higher disturbance precludes the development of organic soils. Similarly, the wetlands along the St. Lawrence River, which are also exposed to flows of greater velocity and energy, are primarily underlain by mineral soils (Fig. 7; also see Environment Canada 1985).

Vegetation complexity

The complexity of wetland vegetation varies among the lakes. The wetland evaluation system (Environment Canada and OMNR 1984) defines vegetation communities and requires that they be mapped. Communities are separated on the basis of number of vegetation forms present (similar to Raunkier life forms; Mueller-Dombois and Ellenberg 1974). The number of vegetation forms in communities differs significantly among the lakes (Table 1; all $P < 0.05$). Analysis of covariance was used to remove the effects of wetland area and number of wetlands in wetland complexes, as vegetation diversity is clearly related to these variables. In general, wetlands along Lake Huron and Georgian bay have more complex vegetation communities than those on Lakes Ontario, Erie, and St. Clair and the St. Lawrence River. The greater amount of swamp habitat and of palustrine site type (Table 1) on Lake Huron and Georgian Bay is related to this greater vegetational complexity. Different elevations and ranges in elevation contribute to this complexity.

Colonial waterbird habitat

The occurrence of colonial nesting waterbirds in coastal wetlands also differs among the lakes (Fig. 8). More wetlands on Lakes Ontario, Erie, and St. Clair support nesting waterbirds than those along Lake Huron and Georgian Bay (Fig. 8). Some noteworthy exceptions exist; for example, Nottawasaga Island near Collingwood supports a large colony of great blue herons (*Ardea herodias*), black-crowned night herons, and, recently, great egrets (*Casmerodius albus*) (also see Weseloh et al. 1986; Smith 1987). Many species reach their range limits in Ontario (Cadman et al. 1987) and are restricted to the lower lakes.

Waterfowl habitat

The critical importance of wetlands of the Great Lakes and St. Lawrence River for waterfowl has been documented by many studies (Dennis and Chandler 1974; Dennis et al. 1984; Ross 1984; Crowder and Bristow 1988). The wetland evaluation system defines various levels of significance for waterfowl

TABLE 1. General characteristics of coastal wetlands on the Great Lakes and St. Lawrence River.

	St. Lawrence River	Lake Ontario	Lakes Erie and St. Clair	Lake Huron	Georgian Bay	Statistically significant difference[a]
Number of wetlands	27	64	28	13	10	N/A
Area of wetlands (ha)	3511	11 555	19 306[b]	1274	1829	N/A
% marsh[c]	91.2	79.1	83.9	5.1	73.3	***[d]
% swamp[c]	8.8	20.3	16.1	27.8	24.6	*[d]
% fen[c]		0.2		16.7	2.1	****[d]
% bog[c]		0.1				N/A
% palustrine and isolated[e]	0.7	2.4	3.9	27.0	4.1	N/A
% riverine[e]	95.8	28.9	3.9	7.0		N/A
% rivermouth[e]	3.5	25.2	16.4	2.2	27.4	N/A
% lacustrine on bay[e]		27.5	13.8	5.2		N/A
% lacustrine[e]		16.6	61.3	58.6	68.5	N/A
% organic soil[b]	6.2	45.4	50.3	31.9	0.0	**[d]
% mineral soil[d]	89.6	53.7	49.7	68.1	100.0	**[d]
Mean total dissolved solids	220.3	339.3	297.5	202.3	195.0	**[d]
Number of vegetation communities	9.1	9.6	6.8	32.2	11.8	***[f]

[a]Statistical tests where appropriate; probability levels: *$0.05 > P > 0.01$; **$0.01 > P > 0.001$; ***$P < 0.001$.
[b]Walpole Island marshes account for at least another 10 000 ha.
[c]Mean value for all wetlands.
[d]Kruskal–Wallis test.
[e]Calculated based on total area in each type for all wetlands.
[f]Analysis of variance with covariates wetland area and number of wetlands in wetland complexes.

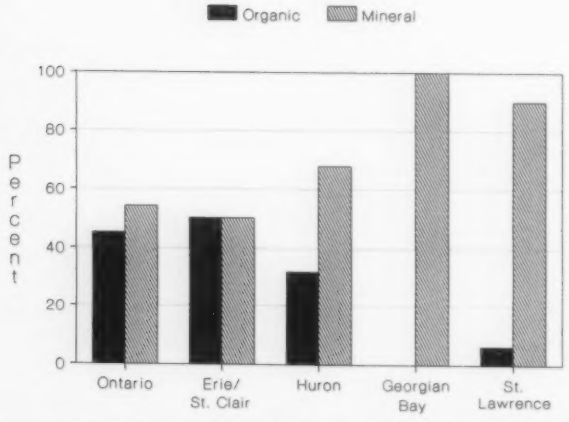


FIG. 7. Average percentage wetland area underlain by organic and mineral soils for the Great Lakes and St. Lawrence River. Percentage of organic and mineral soils is significantly different between lakes (for statistic and P values, see Table 1).

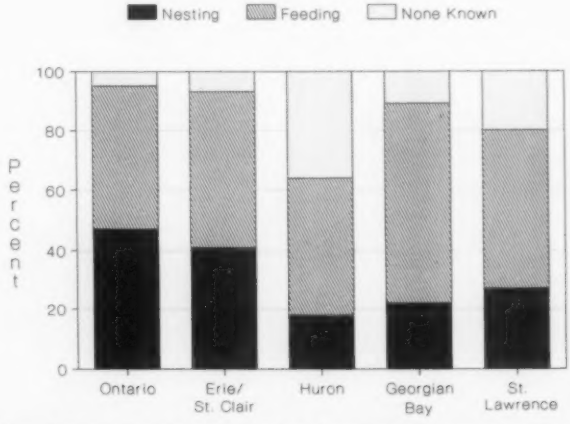


FIG. 8. Presence of habitat for colonial waterbirds in coastal wetlands along the Great Lakes and St. Lawrence River (significant differences, chi-square, $P < 0.01$).

presence and states how these may be determined. An assessment is given of whether the wetland is of national, provincial, regional, or local significance for waterfowl staging and of provincial, regional, local, or no significance for waterfowl production. Three coastal wetlands were assessed as nationally significant for waterfowl staging. Fourteen were considered provincially significant for staging and 6% for waterfowl production. Thirty-one were regionally significant for waterfowl staging and 10% for waterfowl production.

Fish habitat

The importance of Great Lakes coastal wetlands as fish habitat has never been assessed comprehensively. Goodyear et al. (1982) mapped and described known spawning and nursery habitat on both sides of the lakes. Smith (1987) integrated that study with several others to map the more significant fish habitat. More recently, Stephenson (1988, 1989) has shown that coastal wetland habitat is considerably more important for fish reproduction than previously noted.

As with waterfowl, the wetland evaluation system defines various levels of significance for fish spawning and rearing. The importance of spawning and rearing habitat in each wetland may be classified as regionally significant, present, unknown, or unclassifiable. Thirty coastal wetlands were assessed as of regional significance for fish spawning and rearing. However, these and other wetlands might have greater value for fisheries if spawning and nursery values were estimated. OMNR is currently in the process of revising the evaluation system, and fisheries values will receive increased recognition.

Rare and significant species

Rare species contribute to the rating of wetlands in Ontario and are of particular concern to wetland managers (for definition of rare species, see Environment Canada and OMNR 1984). The Great Lakes possess a number of plant and animal species and subspecies that are endemic to the lake waters and shores (Guire and Voss 1963; Campbell et al. 1981; Smith 1987). Some of the plants are considered rare in Ontario and Canada (Argus et al. 1982–88). Records of the occurrence of rare species in wetlands are often taken from secondary sources such as local naturalists, published studies, and other surveys of natural areas. Consequently the inventories of rare species are often incomplete and are frequently updated by OMNR staff as new information becomes available.

Endangered species

Ontario's Endangered Species Act designates 18 species as endangered. The bald eagle (*Haliaeetus leucocephalus alascanus*) occurs at 11 coastal wetlands, primarily along Lake Erie where additional birds are being released into the wild. Formerly the bald eagle was relatively frequent along the Lower Great Lakes shorelines (Brownell and Oldham 1983). The peregrine falcon (*Falco peregrinus anatum*) uses four wetlands during migratory periods.

Bird species

The most frequent of the rare bird species is the black tern which occurs at 68 coastal wetlands. The black tern is also considered threatened in Canada. The marsh wren is nearly as frequent, occurring at 64 wetlands. Forty-four wetlands support least bittern, rare in Canada, and black-crowned night heron. The Caspian tern is found at 32 wetlands, while the common tern (*Sterna hirundo*) frequents 25 coatal wetlands. Twenty-three wetlands harbour the pied-billed grebe (*Podilymbus podiceps*). A number of these species have been shown to occur more frequently in shoreline than in inland wetlands: black tern, marsh wren, Caspian tern, and black-crowned night heron (Glooschenko et al. 1988a). In Ontario, black-crowned night heron and Caspian tern nest primarily on the shores of the Great Lakes (Cadman et al. 1987; Blokpoel 1977; Blokpoel and McKeating 1978; Weseloh et al. 1986).

Reptiles and amphibians

The eastern fox snake (*Elaphe vulpina gloydi*), a subspecies endemic to the Great Lakes coasts, is the most frequently recorded rare reptile, occurring at 18 sites. At 11 wetlands the spotted turtle (*Clemmys guttata*) can be found, and at nine the eastern spiny softshell turtle (*Trionyx spiniferus spiniferus*) has been noted. Massasauga rattlesnakes (*Sistrurus catenatus*) frequent six of the coastal wetlands, primarily those on the Bruce Peninsula. Two wetlands support the Lake Erie water snake (*Nerodia sipedon insularum*), an endangered, endemic subspecies known only from the islands in the western end of Lake Erie (Oldham 1983; King 1986).

Fish species

Coastal wetlands harbour a number of rare fish species, many of which are on the northern edge of their ranges (Campbell et al. 1981; Campbell 1984, 1985; McAllister et al. 1985; Smith 1987). Spotted gar (*Lepisosteus oculatus*), silver chub (*Hybopsis storeriana*), pugnose shiner (*Notropis anogenus*), brindled madtom (*Noturus miurus*), and spotted sucker (*Minytrema melanops*) were recorded at wetlands along Lakes Erie and St. Clair. Undoubtedly, many other rare species frequent waterfront wetlands, and as Stephenson (1988) has shown, further field studies of coastal wetlands for fish habitat use are needed.

Plant species

A number of the endemic Great Lakes plant taxa are found in coastal wetlands. Most of these occur on Lake Huron and Georgian Bay. Many of the Great Lakes' endemic plants are distributed here as well as along Manitoulin Island, the northern portion of Lake Michigan, and extreme eastern Lake Superior (also see Guire and Voss 1963; Morton 1979; Keddy and Keddy 1984). The exceedingly rare Houghton's goldenrod (*Solidago houghtonii*) occurs at one Georgian Bay wetland (Morton 1979; Semple and Ringius 1983). Also along the Lake Huron coast of the Bruce Peninsula, Hill's thistle (*Cirsium hillii*) can be found at three wetland sites, while the dwarf lake iris (*Iris lacustris*) and stiff yellow flax (*Linum medium medium*) occur at one wetland each.

Many southern Carolinian plant taxa reach their range limits along the shores of Lake Erie. Swamp rose mallow (*Hibiscus moscheutos moscheutos*) occurs in 15 wetlands all along the coast of Lakes Erie and St. Clair and the Detroit River. The southern pond lily (*Nuphar advena*) is encountered in 12 wetlands from the Detroit River along Lake Erie and in those along the Lake Ontario coast in the Niagara Peninsula. A number of species have distributions centred on Lake Ontario and are discussed later in that context.

Ordination and Classification

Principal components analysis

Principal components analysis was applied to a matrix of data on 80 wetland sites composed of 36 variables (see Table 2). Some were continuous variables; others were categorical, taking the value 1 or 0, i.e. present or not present. These variables included interspersion and open-water classifications (see Environment Canada and OMNR 1984) as well as the presence of particular plant species, genera, or families as dominants. These variables are listed in the bottom portion of Table 2 (also see Methods of Analysis).

Classification and ordination are both used to examine patterns of variation in ecological communities. The data used in each are similar but the products are quite different. Classification creates statistically based discrete categories. Ordination derives continuous multivariate statistical models of the predominant underlying ecological gradients. The techniques offer

TABLE 2. Principal components analysis of data for 80 coastal wetlands. Factor pattern after varimax rotation. Only loadings >0.35 are shown.

Variable	Principal component 1	2	3	4
Degree-days	−0.675			
% mineral soils		−0.751		−0.361
% organic soils		0.744		−0.360
% fen	0.622		−0.356	
% swamp	0.352	0.656		
% marsh	−0.570	−0.498	0.375	
% isolated and palustrine	0.447			
% riverine		−0.447		
% riverine rivermouth				0.444
% lacustrine rivermouth			0.444	
% protected bay		0.629		
Total dissolved solids				0.681
Vegetation communities				
One form			0.387	
Two forms	0.776		0.365	
Three forms	0.796			
Four forms	0.879			
Five forms	0.813			
Six or more forms	0.514			
Interspersion				
Type 1			−0.477	
Type 2			0.540	
Type 3		0.513		−0.366
Open-water pattern				
Type 1			−0.454	
Type 2 or 3	0.431	0.362		
Type 4			0.397	
Typha	−0.710			
Scirpus	0.383		0.353	
Cyperaceae	0.665			
Juncaceae	0.601			
Larix	0.868			
Thuja	0.903			
Myrica	0.545			
Sarracenia	0.434			
Potentilla	0.642			
Myriophyllum				0.426
Sparangium				0.742
Acer		0.385		
Fraxinus		0.396		
Alnus		0.385		

different descriptions of the same ecological variation. Thus, there are common themes and parallels between the cluster analysis and principal components analysis performed in this study.

The major gradients of variation in coastal wetlands are described by the axes of the principal components analysis (Table 2; Fig. 9). The first axis represents a gradient of climate and vegetation complexity. It primarily separates the wetlands of the Bruce Peninsula from all others (Fig. 9). The occurrence of taxa such as *Thuja*, *Larix*, *Saracenia*, *Potentilla*, Cyperaceae, and Juncaceae are important in defining this first axis, as is the percentage of fen habitat (Table 2). Vegetation complexity is also linked to this axis; the vegetation of wetlands of the Bruce Peninsula is in general more complex structurally than that of other coastal wetlands (Table 2). The percentage of marsh habitat, presence of *Typha* as a dominant, and the number of growing degree-days are all negatively associated with the first axis (Table 2).

The second axis separates lacustrine wetlands on sheltered bays that possess large swamp components and a large proportion of organic soils. Most of these are along Lake Ontario (Table 2). The percentage area with organic soils, swamp habitat, and sheltered bay location contributes most to the second principal component (Table 2). The presence of *Acer*, *Fraxinus*, and *Alnus* also contributes to that axis. It thus suggests a disturbance gradient.

The third axis separates lakeside and rivermouth marshes with simple vegetation structure (Table 2). Principal component 4 suggests a productivity gradient, loading highly on dissolved solids, mineral soils, and rivermouth location (Table 2). Burreed (*Sparganium*) and milfoil (*Myriophyllum*) are the taxa associated with this axis.

These major gradients are similar to those observed in other studies of wetland vegetation (Walker and Wehrhahn 1971; Hutchinson 1975; Keddy 1983; Nilsson 1987; Day et al. 1988). The fertility, disturbance, and water depth gradients so often observed in wetland vegetation are evident in this study. The sampling units in this study are composite wetland units of varying sizes and thus may obscure finer scale variation. Furthermore, only relatively imprecise measures of disturbance and water depth were available to quantify those gradients.

Cluster analysis

Wetland classification can be theoretic, distinguishing between wetland class, form, and type based on general principles (Cowardin et al. 1979; Environment Canada 1987), or empirical based on measured statistical similarity. Two recent initiatives of a theoretic nature are the classification of Great Lakes aquatic habitats (Sly and Busch 1988) and development of a coastal habitat classification for setting conservation priorities (Smith 1987, 1989). The empirical classification developed here will be of use in both initiatives.

The tree diagram derived from cluster analysis of the physical structure (Fig. 10) includes soils, vegetation complexity, and dominant plant species of 80 different wetlands. The variables used are those listed in Table 2, as well as presence–absence of other dominant species (see Methods of Analysis). Ten categories result from the cluster analysis. The major characteristics of the 10 categories are shown in Table 3. Vegetation complexity, site type, and species composition appear to be the important influences on clustering.

The first two major divisions or "branches" in the cluster analysis (groups A, B, and C) (Figure 10; Table 3) isolate riverine wetlands with relatively simple marsh vegetation communities and predominantly mineral soils from other types of wetlands. Group A includes Hoople Creek on the St. Lawrence, Cedar Creek at the west end of Lake Erie, and Jordan Harbour and Eight Mile Creek from the Niagara shoreline of Lake Ontario. Particularly high levels of dissolved solids characterize these wetlands (Table 3). All are subject to considerable runoff from agricultural areas. In group B are a series of small, rivermouth *Typha* marshes from the St. Lawrence and Lakes Ontario and Erie (Table 3). These have very simple vegetation

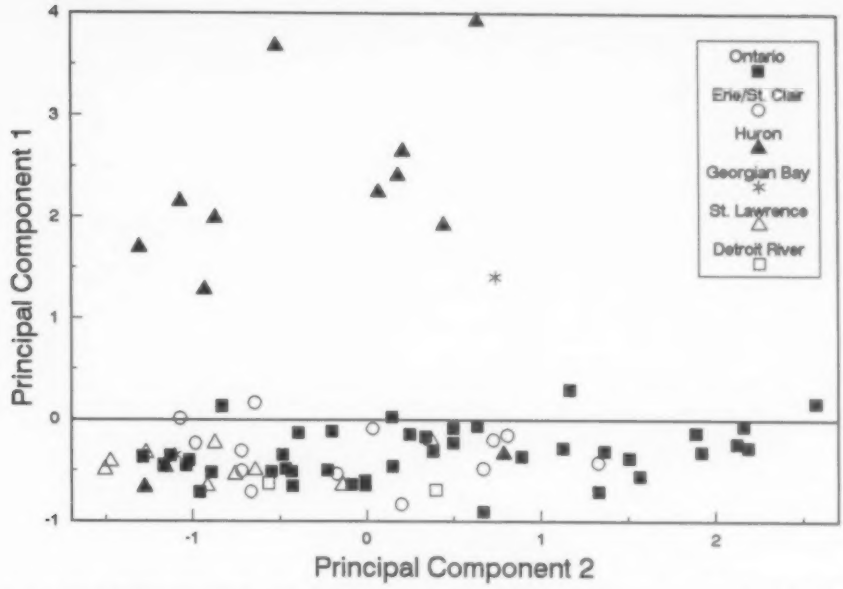


FIG. 9. Two-dimensional ordination of 80 coastal wetlands using principal components analysis. Table 2 indicates the variables contributing to the first two principal components.

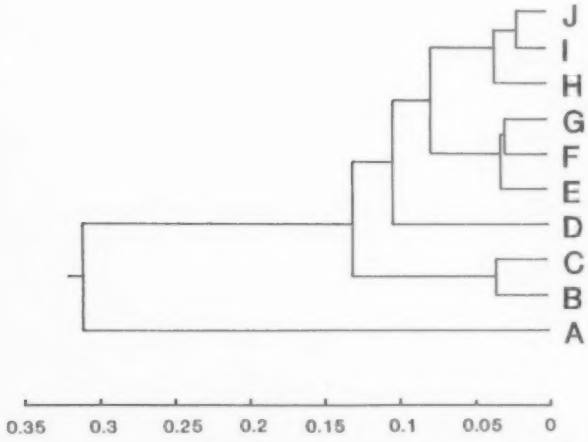


FIG. 10. Tree diagram of the groups derived in a cluster analysis of the physical and vegetation structure and plant species composition of 80 coastal wetlands along the Great Lakes and St. Lawrence River. Letters identify particular categories described in the text and Table 3.

communities. St. Lawrence wetlands and a few others make up group C (Fig. 10), which are predominantly *Typha* marshes with areas of submergents and floating plants such as *Nuphar* as well as occasional swamp components dominated by *Salix*.

Wetlands on protected bays form group D (Table 3). Consequently, the substrates here are on average 85% covered by organic soil, and swamp habitat of *Salix*, *Acer*, and *Fraxinus* make up an average of 35% of the wetland area. Dissolved solids are also generally high. This group could thus be characterized as subject to low levels of disturbance.

Groups E–J (Fig. 10; Table 3) generally have much more complex vegetation structure. Group E wetlands are generally predominantly *Typha* marshes with some communities dominated by *Scirpus*, *Nuphar*, *Nymphaea*, and *Myriophyllum*. They also often possess a swamp component composed of *Salix*, *Cornus*, *Acer*, *Fraxinus*, and *Alnus*. This diversity of species and life forms suggests a large range in water depth for both swamps and marshes. Most lacustrine wetlands fall into group F, primarily those of Lake Ontario, such as Presqu'ile Marshes, but also Kettle Point and Fishing Islands on Lake Huron (Table 3). Many of these wetlands are relatively large. Their marshes contain *Typha*, *Scirpus*, Poaceae, and Cyperaceae. The exposed lacustrine location accounts for this species composition. *Typha* is known to predominate in sheltered locations, while Cyperaceae, Juncaceae, and Poaceae are found in more exposed sites with greater water depth (Hutchinson 1975). *Salix* and *Fraxinus* generally dominate the small adjacent swamps, although *Larix* and *Thuja* occur at the Fishing Islands.

The shoreline fens of Lake Huron and Georgian Bay constitute group G (Table 3). Predominantly lacustrine, these sites also often contain a palustrine component. The vegetation is decidedly northern in affinity (also see Reddoch 1982; Charlton 1986; Charlton and Hilts 1989) with Cyperaceae, Juncaceae, *Thuja*, *Larix*, *Sarracenia*, *Potentilla*, and *Myrica gale* as well as the more typical *Salix* and *Cornus*. *Typha* is not a dominant and is generally absent.

Riverine and rivermouth wetlands with a high percentage of organic soils and complex vegetation structure form group H (Fig. 10; Table 3). These wetlands are located along the Detroit and St. Clair Rivers or along rivers emptying into one of the lakes.

Wetlands with a large percentage of isolated and palustrine site type fall into group I (Fig. 10; Table 3). These include two Bruce Peninsula wetlands and Nut Island Duck Club wetland on Amherst Island, Lake Ontario. The latter contains one of the two coastal bogs among the entire 160 wetlands evaluated.

TABLE 3. Characteristics of categories (A–J) of cluster analysis (see Fig. 10). Mean values are given except for number in category and dominant taxa.

Variable/descriptor	A Rivermouth	B Simple riverine	C St. Lawrence	D Protected bays	E *Typha*	F Lacustrine	G Shoreline fens	H Organic soils	I Palustrine component	J Protected bays
Number in category	4	5	14	7	9	7	9	8	4	9
% organic soil	2.5	0.0	11.1	85.2	31.7	60.8	15.4	84.6	84.7	97.2
Dissolved solids (mg/L)	580	299	186	371	219	181	249	214	198	235
Wetland type										
% marsh	83.5	96.6	93.1	64.5	87.2	87.5	53.0	75.0	53.2	65.9
% swamp	16.5	3.4	6.9	35.5	12.4	11.7	25.7	22.6	41.5	33.1
% fen							20.7	2.4	5.4	
Site type										
% palustrine		11.0	2.3	11.8	1.1		20.8	3.0	30.7	14.4
% riverine	62.3	64.0	95.0	10.3	10.4	3.0	3.1	81.3	4.8	2.2
% rivermouth	37.7	25.0	2.7	1.4	35.2	2.1	1.2	14.3	1.4	1.1
% lacustrine				12.6	11.1	90.9	69.7	1.4	0.7	
% protected bay				63.9	42.2	4.0	3.5		13.3	82.2
Vegetation attributes										
No. of vegetation communities	9.0	4.4	9.1	8.7	14.3	17.1	24.3	11.6	30.0	9.3
Dominant taxa	*Typha*, *Salix*	*Typha*	*Typha*, *Nuphar*, *Salix*	*Typha*, *Salix*, *Acer*, *Fraxinus*	*Typha*, *Scirpus*, *Nuphar*, *Nymphaeae*, *Salix*, *Cornus*	*Typha* *Scirpus*, Poaeaceae, Cyperaceae, *Salix*, *Fraxinus*	Cyperaceae, Junaceae, *Thuja*, *Larix*, *Sarracenia*	*Typha*, *Nuphar*, *Salix*	Cyperaceae, *Cornus*, *Salix*	*Acer*, *Salix*

Group J is similar to group D in having locations on protected bays and high percentages of organic soils and swamp habitat (Table 3). However, group J has a more complex pattern in the spatial arrangement of the vegetation communities or interspersion (see Environment Canada and OMNR 1984).

Conclusions

Our study, drawn from detailed assessment of Ontario's Great Lakes coastal wetlands under the Ontario wetland evaluation system, provides the first summary of important physical and ecological attributes for this coastal wetland habitat. Many patterns reflected in this study corroborate the results of other research on shoreline wetlands and Great Lakes wetlands in particular. The major role of coastal geomorphology and exposure in defining wetland form is known from other studies (e.g. Herdendorf 1987). The presence of disturbance and fertility gradients is typical in shoreline wetland vegetation (Hutchinson 1975; Day et al. 1988). The climatic gradient observed is generally recognized at a biogeographic scale (Whillans 1987). However, the large geographic scale of this study allowed the quantification of the climatic gradient.

Many of these coastal wetlands are class 1 and 2 (provincially significant) or class 3 (regionally significant). Our analyses will be useful to current binational efforts to categorize Great Lakes habitats under the Classification and Inventory of Great Lakes Habitats (CIGLAH) program. They will also assist nongovernmental initiatives to identify and protect critical unprotected coastal habitats. Moreover, our findings contribute to the general ecological knowledge of Ontario's coastal wetlands and suggest areas for further research.

Acknowledgements

We wish to thank all those in OMNR district and regional offices, Environment Canada, and the Conservation Authorities who have assisted in the wetland evaluation effort. In particular we thank John Archbold, Abbe Edelson, Roger Whitwam, Carol-Ann Itel, Ann Misetich, Alex Arifuzzaman, and Amy Stein for technical assistance. Dr. Paul Keddy provided helpful comments on the manuscript.

References

ARGUS, G. W., K. PRYOR, D. J. WHITE, AND C. KEDDY. 1982–88. Atlas of the rare vascular plants of Ontario. Botany Division, National Museum of Natural Sciences, Ottawa, Ont.

AUCLAIR, A. N., A. BOUCHARD, AND J. PAJACZKOWSKI. 1976. Plant standing crop and productivity relations in a *Scirpus–Equisetum* wetland. Ecology 57: 941–952.

BARDECKI, M. J. 1981. Wetland conservation policies in Southern Ontario: a delphi approach. Ph.D. thesis, Department of Geography, York University, Toronto, Ont.

BIRD, E. C. F. 1984. Coasts: an introduction to coastal geography. Basil Blackwell, New York, NY. 320 p.

BLOKPOEL, H. 1977. Gulls and terns nesting in northern Lake Ontario and the upper St. Lawrence River. Can. Wildl. Serv. Prog. Notes No. 75.

BLOKPOEL, H., AND G. MCKEATING. 1978. Fish-eating birds nesting in Canadian Lake Erie and adjacent waters. Can. Wildl. Serv. Prog. Notes No. 87.

BROWNELL, V. R., AND M. J. OLDHAM. 1983. Status report on the bald eagle (*Haliaeetus leucocephalus*) in Canada. Nongame Program Wildlife Branch, Ontario Ministry of Natural Resources, Toronto, Ont.

CADMAN, M., P. EAGLES, AND F. HELLEINER [ED.] 1987. The Ontario breeding bird atlas. University of Waterloo Press, Waterloo, Ont.

CAMPBELL, C. A., B. W. EVERED, D. W. PERIN, M. C. SHARP, AND B. B. WELLER. 1981. The Great Lakes biogeographic province: a Canadian review of source material. The Nature Conservancy of Canada, Toronto, Ont. 2 vol.

CAMPBELL, R. R. 1984. Rare and endangered fishes and marine mammals of Canada: the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) fish and marine mammals subcommittee. Can. Field Nat. 98: 71–74.

1985. Rare and endangered fishes and marine mammals of Canada: (COSEWIC) fish and marine mammals subcommittee status reports: II. Can. Field Nat. 99: 404–408.

CHAPMAN, L., AND D. PUTNAM. 1984. The physiography of southern Ontario. 3rd ed. Spec. Vol. 2. Ontario Geological Survey, Toronto, Ont.

CHARLTON, D. 1986. Ecological studies of Bruce Peninsula wetlands: classification of fens and related wetland types. M.Sc. thesis, Department of Land Resource Science, University of Guelph, Guelph, Ont.

CHARLTON, D. L., AND S. HILTS. 1989. Quantitative evaluation of fen ecosystems on the Bruce Peninsula. Proceedings of the Second Ontario Wetlands Conference. Federation of Ontario Naturalists, Toronto, Ont.

CHRISTIE, W. 1973. A review of the changes in the fish composition of Lake Ontario. Great Lakes Fish. Comm. Tech. Rep. No. 23.

COLLINS, B., AND L. MALTBY. 1984. A statistical analysis of "an evaluation system for wetlands of Ontario, first edition (1983)." Canadian Wildlife Service, Ottawa, Ont.

COWARDIN, L., V. CARTER, F. GOLET, AND E. LAROE. 1979. Classification of wetland and deepwater habitats of the United States. U.S. Fish Wildl. Serv. Publ. FWS/OBS-79/31, Washington, DC.

CROWDER, A. A., AND J. M. BRISTOW. 1988. The future of waterfowl habitats in the Canadian lower Great Lakes wetlands. J. Great Lakes Res. 14: 115–127.

CROWDER, A., B. MCLAUGHLIN, R. WEIR, AND W. CHRISTIE. 1986. Shoreline fauna of the Bay of Quinte, p. 190–200. *In* C. Minns, D. A. Huley, and K. Nichols [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Special Publ. Fish. Aquat. Sci. 86: 270 p.

DAY, R. T., P. A. KEDDY, J. MCNEILL, AND T. CARLETON. 1988. Fertility and disturbance gradients: a summary model for riverine marsh vegetation. Ecology 69: 1044–1054.

DENNIS, D., AND R. CHANDLER. 1974. Waterfowl use of the Ontario shoreline of the southern Great Lakes during migration, p. 58–65. *In* H. Boyd [ed.] Canadian Wildlife Service waterfowl studies in Eastern Canada. Can. Wildl. Serv. Rep. Ser. No. 29.

DENNIS, D., G. MCCULLOUGH, N. NORTH, AND R. ROSS. 1984. An updated assessment of migrant waterfowl use of the Ontario shorelines of the southern Great Lakes, p. 37–42. *In* S. Curtis, D. Dennis, and H. Boyd [ed.] Waterfowl studies in Ontario, 1973–81. Can. Wildl. Serv. Occas. Pap. No. 54.

DENNIS, D., AND N. NORTH. 1984. Waterfowl use of the Lake St. Clair marshes during migration in 1968–69, 1976–77 and 1982, p. 43–52. *In* S. Curtis, D. Dennis, and H. Boyd [ed.] Waterfowl studies in Ontario, 1973–81. Can. Wildl. Serv. Occas. Pap. No. 54.

DRAPER, N., AND V. SMITH. 1984. Applied regression analysis. 2nd ed. Wiley, New York, NY.

ENVIRONMENT CANADA. 1985. Wetlands of the St. Lawrence River region, 1950–1975. Working Pap. No. 45. Lands Directorate, Ottawa, Ont.

1987. The Canadian wetland classification system. Classif. Ser. No. 21.

ENVIRONMENT CANADA AND ONTARIO MINISTRY OF NATURAL RESOURCES. 1984. An evaluation system for wetlands of Ontario south of the precambrian shield. 2nd ed.

FAHSELT, D., AND M. A. MAUN. 1980. A quantitative study of shoreline marsh communities along Lake Huron in Ontario. Can. J. Plant Sci. 60: 669–678.

FRANCIS, G. R., J. J. MAGNUSON, H. A. REGIER, AND D. R. TALHELM. [ED.] 1979. Rehabilitating Great Lakes ecosystem. Great Lakes Fish. Comm. Tech. Rep. No. 37.

GAUCH, H. 1982. Multivariate analysis in community ecology. Cambridge University Press, Cambridge, U.K. 298 p.

GLOOSCHENKO, V. 1983. Development of an evaluation system for wetlands in Southern Ontario. Wetlands 3: 192–200.

1985. Characteristics of provincially significant wetlands as assessed by the Ontario Wetland Evaluation System, p. 187–199. *In* H. Prince and F. D'Itri [ed.] Coastal wetlands. Lewis Publ. Inc., Chelsea, MI.

GLOOSCHENKO, V., J. H. G. ARCHBOLD, AND D. HERMAN. 1988a. The Ontario wetland evaluation system: replicability and bird habitat selection, p. 115–127. *In* D. D. Hook [ed.] The ecology and management of wetlands. Vol. 2. Croom Helm Ltd., Beckenham, Kent, U.K.

GLOOSCHENKO, V., J. ARCHBOLD, AND J. WENINGER. 1987. The importance of swamp wetland habitat in southern Ontario, p. 275–285. *In* C. Rubec and R. Overend [ed.] Proceedings Symposium '87 Wetlands/Peatlands. International Peat Society, National Wetlands Working Group, Canadian Horticultural Peat Harvesters Industry, and Environment Canada, Ottawa, Ont.

GLOOSCHENKO, V., B. PARKER, L. COO, R. KENT, C. WEDELES, A. MASON, J. DAWSON, D. HERMAN, AND P. SMITH. 1988b. Provincially and regionally significant wetlands in southern Ontario. Interim report 1987. Wildlife Branch, Ontario Ministry of Natural Resources, Toronto, Ont.

GOODYEAR, C. D., T. EDSALL, D. ORMSBY DEMPSEY, G. D. MOSS, AND P. POLANSKI. 1982. Atlas of the spawning and nursery areas of the Great Lakes fishes. U.S. Fish Wildl. Serv. Publ. FWS/OBS-82/52, Washington, DC.

GUIRE, K., AND E. VOSS. 1963. Distributions of distinctive shoreline plants in the Great Lakes region. Mich. Bot. 2: 99–114.

HERDENDORF, C. E., S. HARTLEY, AND M. BARNES. 1981. A summary of knowledge of the fish and wildlife resources of the coastal wetlands of the U.S. Great Lakes. Center for Lake Erie Area Research, Ohio State University, Columbus, OH.

HERDENDORF, C. E. 1987. The ecology of the coastal marshes of western Lake Erie: a community profile. National Wetlands Research Center. U.S. Fish Wildl. Serv. U.S. Dep. Inter. Biol. Rep. 85(7.9).

HERDENDORF, C. E., C. N. RAPHAEL, AND E. JAWORSKI. 1986. The ecology of Lake St. Clair wetlands: a community profile. U.S. Fish Wildl. Serv. Biol. Rep. 85(7.7): 187 p.

HUTCHINSON, G. E. 1975. Limnological botany. Vol. 3. A treatise on limnology. John Wiley and Sons, New York, NY.

KEDDY, C., AND P. KEDDY. 1984. Reproductive biology and habitat of *Cirsium pitcheri*. Mich. Bot. 23: 57–67.

KEDDY, P. A. 1983. Shoreline vegetation in Axe Lake, Ontario: effects of exposure on zonation patterns. Ecology 64: 331–344.

KEDDY, P. A., AND A. A. REZNICEK. 1986. Great Lakes vegetation dynamics: the role of fluctuating water levels and buried seeds. J. Great Lakes Res. 12: 25–36.

KING, R. 1986. Population ecology of the Lake Erie water snake *Nerodia sipedon insularum*. Copeia 1986: 757–772.

LACOURSIERE, E. 1969. Étude écologique de la végétation riparienne entre Sainte-Famille et la Pointe d'Argentenaye à l'île d'Orléans. M.A. thesis, Faculty of Forestry and Geodesy, Laval University, Quebec, Que. 150 p.

LEMAY, M., AND G. MULAMOOTTIL. 1984. A study of changing land uses in and around Toronto Waterfront marshes. Urban Ecol. 8: 313–328.

MCALLISTER, D. E., B. J. PARKER, AND P. M. MCKEE. 1985. Rare, endangered and extinct fishes in Canada. Syllogeus 54.

MCCULLOUGH, G. 1981. Wetland losses in Lake St. Clair and Lake Ontario, p. 81–89. *In* A. Champagne [ed.] Proceedings of the Ontario Wetlands Conference. Federation of Ontario Naturalists, Toronto, Ont.

1985. Wetland threats and losses in Lake St. Clair, p. 201–208. *In* H. Prince and F. D'Itri [ed.] Coastal wetlands. Lewis Publ. Inc., Chelsea, MI.

MORTON, J. 1979. Observations on Houghton's goldenrod (*Solidago houghtonii*). Mich. Bot. 18: 31–35.

MUELLER-DOMBOIS, D., AND H. ELLENBERG. 1974. Aims and methods of vegetation ecology. Wiley, New York, NY.

NILSSON, C. 1987. Distribution of stream-edge vegetation along a gradient of current velocity. J. Ecol. 75: 513–522.

OLDHAM, M. J. 1983. An update on the status of the blue racer (*Coluber constrictor foxi*), Lake Erie water snake (*Nerodia sipedon insularum*), Blanchard's cricket frog (*Acris crepitans blanchardi*), and smallmouth salamander (*Ambystoma texanum*) on Pelee Island, Ontario. Wildlife Branch, Ontario Ministry of Natural Resources, Toronto, Ont.

ONTARIO MINISTRY OF NATURAL RESOURCES. 1984. Guidelines for wetlands management. Toronto, Ont.

1987. Guidelines for the preparation of shoreline management plans. Conservation Authorities and Water Management Branch, Toronto, Ont.

PATTERSON, N. J. 1984. An approach to wetland evaluation and assessing cultural stresses on freshwater wetlands in southern Ontario. M.Sc. thesis, I.E.S., University of Toronto, Toronto, Ont. 192 p.

PIELOU, E. 1984. Interpretation of ecological data: a primer on classification and ordination. Wiley, Toronto, Ont.

REDDOCH, J. 1982. Southern Ontario fens. Plant Press 1: 76–78.

REID, R. 1981. A critic's view of wetland policies, p. 98–107. *In* A. Champagne [ed.] Proceedings of the Ontario Wetlands Conference. Federation of Ontario Naturalists, Toronto, Ont.

REID, R. A., N. PATTERSON, L. ARMOUR, AND A. CHAMPAGNE. 1980. A wetland evaluation model for S. Ontario. Federation of Ontario Naturalists, Toronto, Ont. 140 p.

ROSS, R. 1984. Migrant waterfowl use of the major shorelines of eastern Ontario, p. 53–62. *In* S. Curtis, D. Dennis, and H. Boyd [ed.] Waterfowl studies in Ontario, 1973–81. Can. Wildl. Serv. Occas. Pap. No. 54.

SEMPLE, C. J., AND G. S. RINGIUS. 1983. Goldenrods of Ontario, *Solidago* and *Euthamia*. Univ. Waterloo Biol. Ser. 26: 84 p.

SLY, P. G., AND W-D. N. BUSCH. 1988. A system for aquatic habitat classification of lakes. Great Lakes Fishery Commission, Ann Arbor, MI.

SMITH, P. G. R. 1987. Towards the protection of Great Lakes natural heritage areas. Tech. Pap. No. 2. Heritage Resources Centre, University of Waterloo, Waterloo, Ont. 164 p.

1989. Wetlands on the edge: coastal management and Great Lakes coastal wetlands. Proceedings of the Second Ontario Wetlands Conference. Federation of Ontario Naturalists, Toronto, Ont. 8 p.

SNELL, E. A. 1982. An approach to mapping the wetlands of southern Ontario. *In* M. J. Bardecki [ed.] Proceedings, Preconference Session, Ontario Wetland Conference. Occassional Paper. Department of Applied Geography, Ryerson Polytechnical Institute, Toronto, Ont.

1987. Wetland distribution and conversion in southern Ontario. Inland Waters/Lands Directorate, Environment Canada. Working Paper No. 48, Ottawa, Ontario.

STEELE, R., AND J. TORRIE. 1980. Principles and procedures of statistics. A biometrical approach. McGraw-Hill, New York, NY.

STEPHENSON, T. D. 1988. Fish utilization of Toronto area coastal marshes. M.Sc. thesis, University of Toronto, Toronto, Ont.

1989. Significance of Toronto area coastal marshes for fish. Proceedings of the Second Ontario Wetlands Conference. Federation of Ontario Naturalists, Toronto, Ont.

WALKER, B. H., AND C. F. WEHRHAHN. 1971. Relationships between derived vegetation gradients and measured environmental variables in Saskatchewan wetlands. Ecology 52: 85–95.

WESELOH, D., P. MINEAU, S. TEEPLE, H. BLOKPOEL, AND B. RATCLIFF. 1986. Colonial waterbirds nesting in Canadian Lake Huron in 1980. Can. Wildl. Serv. Prog. Notes.

WHILLANS, T. H. 1982. Changes in marsh area along the Canadian shore of Lake Ontario. J. Great Lakes Res. 8: 570–577.

1987. Wetlands and aquatic resources, p. 321–356. *In* M. C. Healy and R. R. Wallace [ed.] Canadian aquatic resources. Can. Bull. Fish. Aquat. Sci. 215: 533 p.

WHITCOMB, M., R. NARRIS, AND R. CARLISLE. 1973. Prince Edward County. Environmental Planning Series, Miscellaneous Report, Parks Planning Branch, Ministry of Natural Resources, Toronto, Ont.

Lake Ontario's Sport Fisheries: Socioeconomic Research Progress and Needs

Tommy L. Brown and Barbara A. Knuth

Cornell University, Department of Natural Resources, Fernow Hall, Ithaca, NY 14853, USA

Fredric C. Menz

Clarkson University, Department of Economics, Pottsdam, NY 13676, USA

Brown, T. L., B. A. Knuth, and F. C. Menz. 1991. Lake Ontario's sport fisheries: socioeconomic research progress and needs. Can. J. Fish. Aquat. Sci. 48: 1595–1601.

The management process of an aquatic system such as Lake Ontario depends on a dynamic information base and occurs within an environment comprising ecological, social, cultural, political, and economic factors. It is critical that this information base include socioeconomic components pertaining to resource user values and behaviors as well as the traditional ecological components. This paper reviews socioeconomic information pertaining to the utilization and valuation of Lake Ontario's sport fisheries. It also examines the socioeconomic components of assessing the risks to humans posed by contaminants present in sport fish, communicating this information to fish consumers, and monitoring and understanding human responses to these communications. Several studies have examined the economic impacts of sport fishing on coastal communities of Lake Ontario. Few studies have examined the net economic value of sportfishing to anglers, or how contaminants have reduced such values. Similarly, few studies have examined how the public responds to information about contaminants in sport fish. Some research in these areas is currently underway.

Pour gérer un milieu aquatique comme le lac Ontario, il faut disposer d'un ensemble d'informations pertinentes et à jour et prendre en considération une série de facteurs écologiques, sociaux, culturels, politiques et économiques. Il est essentiel de tenir compte des composantes socio-économiques relatives aux valeurs et aux comportements des utilisateurs du lac de même que des composantes écologiques classiques. Cet article traite des données socio-économiques relatives à la pratique et à la gestion de la pêche sportive dans le lac Ontario. Il examine aussi les enjeux socio-économiques entrant dans l'évaluation des risques pour la santé que représentent les contaminants touchant cette activité, la communication des résultats d'une telle évaluation aux consommateurs de poisson et l'observation et la compréhension des réactions du public face à ces informations. Plusieurs études ont porté sur les impacts économiques de la pêche sportive sur les populations riveraines du lac Ontario. En revanche, peu d'études ont examiné la valeur économique nette de cette activité pour les pêcheurs à la ligne, ou dans quelle mesure les contaminants ont pu réduire cette valeur. De même, les réactions du public aux informations sur les contaminants touchant les poissons ont été très peu étudiées. Ces questions font actuellement l'objet de recherches.

Received January 24, 1989
Accepted June 26, 1990
(JA027)

Reçu le 24 janvier 1989
Accepté le 26 juin 1990

Lake Ontario, one of the Great Lakes, is one of the largest aquatic freshwater resources in the world. It has been studied largely as an aquatic biological and physical system, with most research examining individual biological/ecological components and their linkage to one or perhaps two other components. Particular attention has been given to its fisheries, to nutrient enrichment, and to toxic contaminants. While there is a great deal of unfinished research on these topics, we probably have a deeper understanding of the biological/ecological and physical aspects of Lake Ontario than of socioeconomic aspects such as the economic value of the components of the ecosystem, relative values of stocks of alternative species, the comparative impacts on local communities, satisfactions of those who use the resource for recreation and as a food supply, and how contaminants found in the lake's fish and drinking water affect the behavior of resource users.

Socioeconomic information and the linkages between the socioeconomic and biological/physical aspects are crucial to a variety of management and policy decisions regarding the Lake Ontario fisheries resource. Krueger et al. (1986) have portrayed resource management as occurring in an environment involving a cyclic process in which agency goals and objectives are established, problems are identified, actions taken, and results evaluated, leading back to a reexamination of goals and objectives. The management process depends on a dynamic information base, and occurs within an environment comprising ecological, social, cultural, political, and economic factors. It is critical that this information base include socioeconomic components pertaining to resource user values and behaviors as well as the traditional ecological components. Beyond static resource user and ecological characteristics, the information base should provide for an understanding of interactions between the biological/physical and the socioeconomic systems. For example, angler perceptions of contaminants and water quality may strongly affect their fishing behavior for certain species, which may in turn affect the populations and age structure of those species and related components of the lake ecosystem.

This paper provides a review of the available socioeconomic information pertaining to the utilization and valuation of the Lake Ontario sport fisheries resources and suggestions for the direction of future research. The first section examines the utilization of the fisheries, the economic impacts of the fisheries and value of the fisheries to anglers, and marketing, communications, and educational efforts. The second section examines the interplay between assessing the contaminants present in the fisheries and their risks to humans, policies communicating this information to anglers and other potential consumers of Lake Ontario fish, and the responses of the public to the communications regarding contaminants in fish. Much of the available information is from the United States side of Lake Ontario. Canadian data to which we have access have been included.

Utilization and Valuation of Lake Ontario Sport Fisheries

Based on American and Canadian national surveys, Lake Ontario in combination with the Niagara and St. Lawrence Rivers experienced approximately 9.6 million angler days in 1980 (D. R. Talhelm, Department of Park and Recreation Resources, Michigan State University, East Lansing, MI, unpublished data). About 5.3 million angler days, or 55% of the total, occurred in New York, with the remaining 4.3 million angler days occurring in waters of the Province of Ontario. Among the five Great Lakes, fishing pressure on Lake Ontario was second lightest after Lake Superior.

From unpublished 1985 data from the U.S. Survey of Fishing, Hunting, and Associated Wildlife Recreation, conducted by the U.S. Fish and Wildlife Service (USFWS), approximately 4.16 million angler days were spent on the New York portion of Lake Ontario (exclusive of the Niagara and St. Lawrence rivers and Lake Ontario tributaries). About 2.75 million of these days were by boat and 1.42 million from shore. This level of sportfishing represents a dramatic increase from 1973 when the total effort for Lake Ontario was estimated at 664 000 angler days (Brown ca. 1973).

Economists differentiate between two major types of resource values that are conceptually quite different: (1) expenditures that result in jobs and additional income to people in a defined geographic area and (2) the net value of the experience to the individual, which is the difference between the amount of total value received and the individual's expenditures. Regarding the first type of values, Lake Ontario researchers have examined economic impacts of salmon fishing on communities along the Salmon River in Oswego County; the impacts of the Empire State/Lake Ontario (ESLO) derby on a several-county area, and the total spending impacts of all Lake Ontario fishing on coastal communities. In general, these studies have measured only the direct spending or employment impacts and not the indirect and induced (so-called "multiplier") effects of this "first round" spending by anglers.

Net values of the fishery to individuals, or the consumers surplus, cannot be observed directly in the market place. As a result, they are difficult to estimate accurately. Net values are especially useful in two situations, however. First, if a particular fishery were threatened by another use of the lake such as an industry or shoreline development, the net values of the two competing uses could be compared to determine which is of greater economic value to society. Second, if a fishery is threatened by another species such as the sea lamprey, the net value of the fishery can be compared with the cost of sea lamprey control for public policymaking. Very few studies have estimated net economic values of Lake Ontario fisheries. A summary of information on the economic values of Lake Ontario follows.

Economic Impact Studies

Information on expenditures of anglers fishing New York's Great Lakes dates from 1973, when anglers spent approximately $10.2 million at fishing sites along the entire New York Great Lakes system (including the Niagara and St. Lawrence rivers) (Brown 1977). Of this total, ony $1.8 million was spent by anglers fishing Lake Ontario proper, and an additional $675 500 was spent by anglers fishing the bays, estuaries, and tributaries of Lake Ontario (Brown ca. 1973). The total fishing effort for the Lake Ontario system was estimated at 972 000 days; thus, on-site expenditures were approximately $2.55 per day (this does not include fishing equipment).

The above data provide a baseline for examining the ensuing economic impacts of the developing salmonid fisheries in Lake Ontario. Pacific salmon were introduced in Lake Ontario in the late 1960s, but the absence of sea lamprey controls eliminated the visible presence of coho and chinook salmon until 1973, when the first fall runs were documented on the Salmon River. In the fall of 1973, anglers took approximately 5680 trips to the Salmon River and spent $62 100 (Brown 1976a). The impacts of salmon fishing outside the Salmon River in 1973 were negligible.

While salmonid populations were being established in the early to mid-1970s, stocking was heaviest on the Salmon River, which also experienced the heaviest return spawning migrations. As a result, research efforts were concentrated there. By 1975, angler expenditures during the fall salmon runs grew to an estimated $411 800, and the first growth and expansion in new businesses was documented (Brown 1976a). Expenditures per angler day in Oswego County increased from $10.93 in 1973 to $19.61 in 1975. By 1975, some initial impacts of salmon fishing were also noted from spring fishing along the central shoreline of Lake Ontario, although data are not available.

The discovery of PCB and mirex contamination in fish forced the virtual closing of salmonid fishing in 1976, as the New York State Department of Environmental Conservation (DEC) issued a ban on possession. The number of angler trips dropped by 70% from the 1975 level (Brown 1976b). The stocking of salmonids was discontinued in 1977, and salmon fishing impacts were not documented again until 1980. It was for the overlap period of April 1976 through March 1977 (with the ban on salmonid possession declared on September 16, 1976) that New York's second statewide mail survey of anglers was conducted. That study estimated a total of 1 027 000 angler days on Lake Ontario, up substantially from the estimate of 664 000 angler days in 1973. Expenditures of anglers at Lake Ontario communities increased from $1.8 million in 1973 to $4.5 million 1976–77 (Kretser and Klatt 1981). It should be noted that the 1976–77 results may be inflated relative to 1973 results because the response rate to the 1976–77 survey was notably lower than in 1973.

By 1978 the impacts of Lake Ontario's resumed salmonid fisheries were felt almost lakewide. The first ESLO derby was held, and in 4 days, anglers spent over $483 000, more than was spent in conjunction with the entire fall salmon runs on the Salmon River in 1975. Lakewide expenditures for the ESLO

derby were estimated in excess of $1.5 million in 1980. They grew to $2.9 million in 1982, $3.8 million in 1984, $4.8 million in 1986, and $6.0 million in 1988 (Wayne County Public Information Office 1988).

A comprehensive survey of New York's Lake Ontario fishing effort and economic impacts was conducted in 1984 by means of a year-long roving creel census with a follow-up mail survey to obtain expenditure data. Total angler trips (defined as a single outing to a particular site), including tributaries, were estimated at 936 153. This vastly underestimates the 1985 USFWS estimate of 4.16 million angler days, excluding tributaries. It is not unusual for estimates based on at-home interviews (such as the USFWS study) to differ markedly from creel census estimates. A creel census of a large area cannot hope to provide total year-round coverage of fishing on waters of the magnitude of New York's Great Lakes system. As a specific example, open-water and embayment boat fishing and shore and pier fishing were estimated only for the months of April through October. However, the USFWS survey, which requested memory recall data for an entire year, is almost certainly upward biased.

From the 1984 creel census, almost 40% of the total effort was open-lake fishing, about 30% was from tributaries, 19% from shore and pier fishing, and the remainder from fishing in embayments and around power plant discharges. Of the total trip expenditures of approximately $32 million, $24.5 million were made in counties bordering Lake Ontario. About 58% of these expenditures occurred in the eastern section of the lake in Jefferson, Oswego, and Cayuga counties, with over 40% in Oswego County alone. About 27% of total expenditures were in the Greater Rochester area (Monroe and Wayne counties), and 17% were in the western Lake Ontario counties of Niagara and Orleans (Dawson 1986).

An analysis of Lake Ontario fishing was undertaken from data supplied by the USFWS from their 1985 national survey of fishing, hunting, and associated wildlife recreation. The 1985 survey asked for days fished on Lake Ontario specifically, days fished on Great Lakes tributaries generally, and expenditures for Great Lakes fishing generally. Total trip expenditures for the 2.985 million angler days represented by anglers who fished Lake Ontario but not Lake Erie or the St. Lawrence River were $51.2 million, or $20.50 per day. The true estimate of total trip expenditures lies between $51.2 million and $78.2 million, which is the total New York Great Lakes expenditures of anglers who fished Lake Ontario, but who may have also fished Lake Erie or the St. Lawrence River. Anglers who fished Great Lakes waters in addition to Lake Ontario had smaller travel expenditures per day than those who fished only Lake Ontario. Therefore, the estimate of total Lake Ontario expenditures cannot be further refined.

Considering that these 1985 angler expenditures do not include those of anglers who fish Lake Ontario tributaries but not the open lake, and that DEC boat censuses in 1986 and 1987 have continued to show increases in effort, it is highly likely that sportfishing on the New York side of Lake Ontario now represents an "industry" on the order of $100 million annually. Current Canadian data are not available. However, in 1980, total effort on the Canadian side of Lake Ontario (incuding the St. Lawrence and Niagara rivers) was about 81% that of the American side of the same waterways (derived by D. R. Talhelm from a Canadian national study).

The above studies have examined only the total direct spending of anglers. Planners and economists are also concerned about the amount of spending by anglers residing outside the region in question, for this represents new moneys infused into local or regional economies. It is also legitimate, however, to consider the degree to which an expanding fishery keeps resident anglers at local sites rather than traveling to other fisheries outside the region. The degree to which Lake Ontario's fisheries have kept resident anglers at home who would otherwise have exported money to other regions has not been investigated.

In addition to direct spending impacts that result when nonresident anglers visit Lake Ontario communities, businesses that serve anglers purchase additional commodities from other local businesses in order to serve anglers. For example, restaurants may buy more breads or pastries baked at local bakeries or more fresh fruits and produce from local farmers. These are known as *indirect impacts*. Further, employees of these local businesses who receive wages paid by anglers spend a portion of those wages locally. This creates *induced impacts*. The concept of *multipliers* has been developed as a measure of the ratio of the direct, indirect, and induced changes of economic activity to the direct impact itself (Archer 1976). In general, the larger the defined region and the more diversified its economy, the more businesses and employees will buy from other businesses within the region, and the larger the multiplier will be.

Martin (1987) has estimated directly a multiplier associated with sportfishing on Lake Ontario. Using the Bay of Quinte region at the northeastern end of Lake Ontario which contains four counties in the Province of Ontario, Martin used a modified Keynesian multiplier to estimate the direct, indirect, and induced income generated by visiting walleye anglers, associated spending by the Ontario Ministry of Natural Resources, and the local private sector. Using minimum estimates generated in confidence intervals, which were roughly 20% lower than maximum estimates, Martin found that $4.4 million in total expenditures generated $752 658 in direct income, or $925 769 in combination direct, indirect, and induced income to employees. The latter figure represents an income "normal" multiplier of 0.209. Thus, each dollar of angler expenditures generated 20.9 cents of wages to employees in the Bay of Quinte region. Multipliers of this magnitude are typical of regions with small urban areas; many of the inputs to local businesses must be purchased from outside the region. Multipliers for metropolitan centers along Lake Ontario such as Toronto or Rochester would be much larger.

Economic impacts can be measured by changes in employment as well as in spending. In a recent analysis of 1975, 1980, and 1985 state employment data from New York's coastal areas, Connelly and Brown (1988) found that the number of tourism-related firms increased from approximately 1700 in 1975 to 3808 in 1985. Employment increased from approximately 18 300 in 1975 to 42 405 in 1985. A highly disproportionate amount of these firms and employment were in the coastal portions of Great Lakes counties. Although we cannot estimate quantitatively the proportion of this employment growth that is attributable to the Great Lakes fisheries, these fisheries are the only readily identifiable growth component affecting Great Lakes tourism.

Examining seasonal aspects of tourism provides substantial evidence that much of the growth in tourism along Lake Ontario is related to the Great Lakes fisheries. In the northeastern United States, typical seasonality curves in areas of high tourism will show a summer employment peak in tourism-related sectors that is 2 to 5 times the magnitude of employment in the spring and late fall. Along the Great Lakes coast, the summer season-

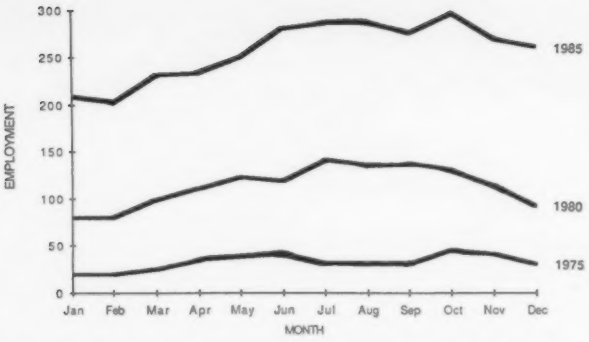


FIG. 1. Employment in tourism-related sectors near the Salmon River, 1975–85.

ality coefficient (employment of the highest summer month divided by that of the lowest nonsummer month) was 2.2 for the Amusement and Recreation Services sector, which contains many outdoor facilities that are open only in summer, but less than 2.0 for the 11 other identified tourism sectors (Connelly and Brown 1988). Furthermore, seasonality in employment decreased from 1975 to 1985 as the impact of the fisheries increased. This would be expected because much of the impact of fishing-related tourism on the Great Lakes occurs in the nonsummer months.

The growth in tourism and the low degree of seasonality along Lake Ontario is illustrated by depicting monthly employment (data obtained from the New York State Department of Labor) in 1975, 1980, and 1985 for the Salmon River area in Oswego County (Fig. 1). Tourism employment grew from an average of 25 to 35 employees per month in 1975 to over 200 employees per month during each month of 1985. The slight seasonal employment peak that exists in this area occurs in October, corresponding to the salmon runs in the Salmon River.

Economic Valuation Studies

Very little effort has been devoted to estimating the economic value of Lake Ontario fishing to the anglers themselves. Such studies are important to understanding the overall magnitude of the value of Lake Ontario fisheries and of particular types of fishing experiences (i.e. fishing for particular species, tributary versus open-lake boat fishing versus shore or pier fishing). This information is particularly important in evaluating public policy and projects affecting alternative uses of fishery resources.

Using the 1976–77 DEC statewise survey, Brown (1982) used a variation of the travel cost technique to estimate the value of the Great Lakes fisheries. This analysis estimated that the net economic benefits to anglers of the 957 300 angler days during this 12-mo period were $26.47 million, or $27.65 per angler day (in 1982 dollars). These data were collected during a 12-mo period in which there was a ban on the possession of salmon from September through March, but it was nevertheless notable that 94% of the total net benefits of fishing on Lake Ontario were attributable to warmwater fishing trips, and over 60% of the benefits occurred in the Jefferson County portion of Lake Ontario. We would expect such estimates to be markedly different today with the lake's salmonid fisheries.

Using the same data source, Menz and Wilton (1983) also used a variation of the travel cost method to infer the net economic value of the eastern Lake Ontario — St. Lawrence River bass fishery. Their analysis estimated per diem values ranging from $15.43 to $35.22 in 1976, depending on the specific angling site. The net economic value of the bass fishery to licensed New York resident anglers was estimated to be $18.4 million. The most important implication of this analysis probably is the economic documentation of the extremely important warmwater fisheries in Lake Ontario, especially those in the eastern basin.

Marketing, Communications, and Education

One of the primary justifications for introducing salmonids into Lake Ontario was the tremendous potential economic impact for local communities. While the potential economic impacts were very real, just as real were the ensuing problems of parking, traffic congestion, fishing access, garbage clean-up, and provision of a variety of services sought by anglers. In New York, the primary educational resources that worked with communities to help them plan for and take advantage of the benefits of the influx of anglers while minimizing the associated costs were the Sea Grant Extension program and Cooperative Extension. These programs worked to identify research needs and to interpret research results to Lake Ontario communities. Educational efforts included both information on the economic impacts of the fisheries and on means of cleaning and cooking salmonids that minimize human ingestion of contaminants (Schuman et al. 1979).

As the salmonid fisheries and associated community services developed, communities and entrepreneurs became eager to promote and market Lake Ontario's fisheries more strongly. Brown (ca. 1982) analyzed the number of visitors to various counties along Lake Ontario and their associated expenditures by major media regions of residence. These media regions corresponded as closely as possible to groups of counties that were dominanted by a newspaper and television stations from a given metropolitan area. For example, the Rochester area was the heaviest contributor to angler spending in eastern Lake Ontario.

Chemical Risk Management and Socioeconomic Considerations

Approaches to Risk Assessment and Risk Management

Economic benefits derived from Lake Ontario sport fisheries are potentially decreased due to the presence of chemical contaminants in the water and in fish flesh. Environmental managers are faced with the challenge of addressing both the economic needs of Lake Ontario communities and the need to develop mechanisms for keeping human health risks from chemical contaminants under some acceptable limits. The Lake Ontario Toxics Committee (1988) recognized that elevated levels of contaminants interfere with the safe consumption of affected fish and lead to changes in sportfishing participation and associated economic impacts. As a result, it has selected the resumption of using fish as a safe food source as one long-term ecosystem remediation goal.

In the short term, however, before complete remediation is achieved, alternative management strategies are needed to protect human health. Actions based on these strategies involve two approaches, risk assessment and risk management. Both are information-intensive processes. Risk assessment is a scientifically based process to calculate the probabilities of adverse effects from exposure to chemical contaminants. Risk management involves deciding on and implementing appropriate actions to respond to those risk probabilities, and

includes interpretation of risk assessment results in light of social, political, economic, and legal factors. Risk managers often evaluate risks in terms of potential costs and benefits associated with taking the risk, including the benefits and costs of recreational participation in sport fisheries and effects on local economies. Lake Ontario fisheries management and health agencies often both become involved in these two processes. The outcome is preparation and distribution of recommendations or "health advisories" which include suggested maximum levels of sport fish consumption consistent with protecting human health.

Risk Assessment

Risk estimates, conducted through a variety of mathematical modeling approaches, consider the toxicity of one or more chemicals and the routes and magnitude of human exposure to the contaminants (Safe Drinking Water Committee 1980). The information base for Lake Ontario contaminant risk assessment relies on data from laboratory tests, as well as from field tests on Lake Ontario and other Great Lakes (e.g. Bro et al. 1987).

Because information on impacts of chemical contaminants on human health is incomplete, a series of assumptions is made in risk assessments (e.g. Crouch and Wilson 1979). These assumptions influence the confidence with which later risk management decisions can be made, and thus influence the perceptions and responses of sport fishery users asked to comply with risk management decisions.

For Lake Ontario, assumptions which increase the uncertainties in management decisions arise from the extrapolations and assumptions from sampling techniques and laboratory data. Human health effects are generally assessed from laboratory tests using animals exposed to high levels of chemicals for short time periods, unlike the long-term exposures at low levels more typical in humans exposed to Great Lakes contaminants (Sonzogni and Swain 1984). When risks assessed from short-term data are extrapolated to exposures experienced by sport fish consumers, predicted carcinogenic effects can vary by several orders of magnitude (Park and Snee 1983). Exposure also is usually considered to remain constant over a lifetime, when in reality concentrations of many environmental contaminants are decreasing (Sonzogni 1987). Further, analytical results generated from chemical analyses of fish tissue vary depending on the preparation technique used. New York uses a standard fillet technique whereas the Ontario Ministry of the Environment uses a different edible portion sample method. One comparative study indicated that the standard fillet techniques would produce values for certain pesticides that can be close to twice the values produced by the edible portion method (Lake Ontario Committee 1987). While efforts are underway to develop consistent health advisories for the Great Lakes under the Great Lakes Toxic Substances Agreement signed by the U.S. Great Lakes governors in May 1986, use of different sampling protocols and analytical techniques in risk assessment remains an impediment to full coordination and consistency.

For Lake Ontario sport fish risk assessments, one of the uncertainties is human consumption rates of sport-caught fish. Average fish consumption rates vary by cultural subpopulations and geographic locations from about 6 to 100 g/d, and high levels of consumption may approach 165 g/d (PTI Environmental Services 1987). While various angler surveys indicate the importance to anglers of consuming their catch, little is known about the contribution that sport-caught fish make to the diet of Lake Ontario basin residents. Data from the Lake Michigan area show median sport fish consumption levels of 15 kg/yr, compared with the national per capita average for all seafood consumption of 6.8 kg/yr (Bro et al. 1987). Hence, assumptions about the appropriate human exposure data for risk assessments could be improved by identifying actual sport fish consumption of Lake Ontario basin residents. In conducting its risk assessments, New York normally assumes a lifetime (70 yr) consumption of one meal (0.5 lb or 231 g) per week of sport fish (J. Colquhoun, New York Department of Environmental Conservation, personal communication, May 1988).

The most trustworthy sources of information on adverse human health effects from chemical contaminants in fish are epidemiological studies relating known exposure and dose levels to documented human health responses (Bro et al. 1987). Unfortunately, no such epidemiological data exist for consumers of Lake Ontario sport fish.

Risk Management

Risk management involves a conscious decision to design and implement policies directed toward the reduction of risk for some segment of the exposed population. The bases for these decisions are the risk assessment procedures described above. Risk assessments are translated into a variety of management strategies, each with its own set of information needs.

Risk management in sport fisheries involves a complex of different mandatory nad voluntary schemes, in contrast with commercial fisheries in which consumers of fish obtained in the commercial marketplace have no easy access to information regarding the harvest location of the fish being purchased, nor about the presence of contaminants in those environments. Consequently, for commercial fisheries, agencies such as the Food and Drug Administration in the United States and Health and Welfare in Canada set allowable chemical contaminant levels for fish entering the commercial marketplace. Risk management in sport fisheries differs from that in commercial fisheries due to the assumption that fish consumption by sport anglers is a more voluntary activity, with anglers having full knowledge of the species consumed, the environment in which the fish was caught, and the likelihood of chemical contamination. This assumption holds for informed recreational anglers only. The uninformed may still be engaging in an involuntary exposure to chemical contaminants.

The first action taken to address the problem of contaminants in sport fish in New York waters was an advisory issued in 1971 to eat no more than one meal of fish per week from any waters in the state. This was followed in 1976 by the first major contaminant management action specific to Lake Ontario, a ban on the possession of any of seven species of fish from the lake, instituted by DEC. The action was greeted with mixed reaction by the angling public, and the New York tourism industry. Anglers' comments included questioning the underlying political reasons for the ban, and emphasized the need to keep citizens informed about reasons for policy changes affecting the fisheries (Brown 1976b).

The full economic impacts of the ban are unknown, but data from a statewide angler survey, conducted on a sample of 1976–77 fishing license holders, indicated that 24% of resident anglers and 12% of nonresident anglers fished less in Lake Ontario waters due to the ban on fish possession than they would have without the ban (Kretser and Klatt 1981). Given an estimate of total expenditures associated with Lake Ontario fishing in 1976–

77 of $19.9 million (Kretser and Klatt 1981), the lost economic impact due to the ban was likely substantial. Of total expenditures, $4.5 million occurred in local Lake Ontario communities. For the Salmon River alone, based on an estimated 60–70% reduction in fishing after the ban (Brown 1976b), Skinner (1979) estimated that the minimum economic loss due to the ban was $329 500 in 1976. DEC (1985) later suggested that the probable economic loss due to the ban, for the total Lake Ontario fishery, was in the millions of dollars from 1976 to 1978.

A complete ban on fish possession is one management strategy to protect public health. The economic impacts of such a mandatory closure are likely to be much more substantial than strategies designed to elicit voluntary compliance with recommendations. These alternative management actions rely on information and education to allow anglers to continue fishing and make a reasoned decision regarding consumption of the caught fish. Kretser and Klatt (1981) found that 71% of anglers surveyed preferred some combination of health hazard warnings and fish consumption recommendations rather than mandatory closures. Anglers wish to be allowed to make a decision whether or not to participate in a contaminated fishery, and to what extent. The key here is that anglers must have complete information about the potential presence of contaminants in the fish they catch, as well as the potential health risks of consuming those fish.

In response to public comments and the need to coordinate its activities with the Department of Health, DEC (1985) established an explicit policy statement to explain how it will respond to knowledge about chemical contamination of fish. The statement includes as a goal the protection of the public health and encouragement of the beneficial uses of fishery resources, both commercial and recreational.

Health advisories are also issued by the Ministries of Environment and Natural Resources in Canada (Ministry of the Environment 1987). While New York issues an advisory only in the event that a species tested exceeds a consumption criterion, and includes an "eat no more than one meal per week" caveat for any waters of the state, Ontario issues all statistically valid fish contaminant data for situations in which contaminant criteria are both exceeded and not exceeded.

In addition to possession bans and consumption advisories that focus on modifying human behavior, managing contaminated fisheries can take a biological focus. Stocking strategies may be modified to emphasize smaller, short-lived, or less fatty species less likely to accumulate contaminants. In Lake Ontario, bottom feeders and salmonids are most affected by contaminants. Salmonids are the species most preferred by anglers. A stocking pattern to decrease emphasis on these species because of contaminants would likely receive much public opposition.

Few data are available to estimate the economic impact the advisories have had on the Lake Ontario fishery. DEC (1985) noted that much of the economic loss due to advisories may be experienced by local economies through displacement of fishing activities to other areas, other activities, or through nonexpenditure of funds. Some impact on local commerce is probable where contaminated fisheries are known and publicized, yet the salmon fishery on the Salmon River (for which consumption advisories exist) stimulated angler trip expenditures of $6.1 million in 1984 (Dawson 1986). We know of no studies that have addressed the losses in net economic value to anglers resulting from diminished angling opportunities due to the advisories.

In addition, few studies have assessed angler reaction to the consumption advisories to determine if anglers are aware of the advisories, or if knowledge of the advisories has led to the desired behavioral changes such as reduced consumption of certain sizes or species of fish caught in Lake Ontario. The Ontario Ministry of the Environment has conducted three surveys to assess the usefulness of the *Guide to Eating Ontario Sport Fish* (Cox et al. 1987). These questionnaires were distributed either with the guide, or to known recipients of the guide, so no data are available regarding the numbers of Ontario anglers who were not reached with consumption advisory information.

Results of the 1986 questionnaire indicated that 48.9% of the respondents changed their fishing and/or fish-consuming habits as a result of the guide (Cox et al. 1987). These behaviors included eating less fish, eating fish only within the guidelines, returning larger fish and eating smaller fish, and completely stopping fish consumption. Unfortunately, data regarding the reasons for not changing are not available for the remaining 51.1% of respondents who did not change their habits. This type of information is critical to evaluating the effectiveness of risk management communications such as the guide.

M. E. Wendt (unpublished Master of Science thesis (1986), Cornell University, Ithaca, NY. 244 p.) evaluated the awareness among fish-consuming low-income women in New York, living near Lake Ontario, about fish consumption guidelines issued in the fishing regulations booklet. She concluded there was a lack of knowledge about the existence of the guidelines, and a general misunderstanding of the potential effects of chemical contaminants in the diet.

Research Needs and Ongoing Efforts

Economic and Social Impacts

Compared with many major lake fisheries, we have a good base of economic impact data related to Lake Ontario fishing. Yet, little information is available to assess the true impacts of environmental changes or changes in fisheries policies. For example, we do not have enough data to assess the impacts of contaminants in the Great Lakes on fishing effort, or the resulting loss in revenues or employment that would accrue to coastal communities. Furthermore, the policy of allowing snagging of salmon is controversial. Substantial amounts of unruly as well as illegal behavior typically accompany snagging. DEC feels some pressure to cut back on the sections of streams where snagging is now permitted and eventually to eliminate snagging. If snagging were banned on the Salmon River and other Lake Ontario tributaries, it is not clear whether those who now snag for salmon would continue to fish or would discontinue fishing for salmon. Nor is it clear how many traditional anglers who do not like snagging would be attracted to a fall salmon run if no snagging were allowed. Revised snagging regulations will undoubtedly have important economic impacts. Some research is underway to develop an understanding of the fishing patterns and attitudes of anglers who snag for salmon and the economic impacts of their activities.

Economic Values

New York has had a number of environmental calamities that have affected the state's fisheries, especially in the past 15 yr. Mirex and PCBs, oil spills, and acid precipitation are but a few

examples. Whenever such calamities occur, information on the value of the fishery and of the portion that is affected is needed to assess costs of restoration and mitigation, and/or to determine natural resource damages. Past Lake Ontario and other angler studies have been designed to estimate economic impacts, but not the net economic value of the fisheries to anglers, nor the reduction in economic value to anglers and others from environmental quality degradation. The 1988 New York statewide angler survey has been designed to allow net economic values to anglers to be estimated for major sport fisheries of the state such as Lake Ontario. Information on nonuser values (existence and option values) of the fishery and other components of the freshwater ecosystem would also be valuable in evaluating alternative policies for managing the Lake Ontario sport fishery.

Other useful information on economic values involves maximizing economic benefits subject to biological constraints. There are a large number of possible stocking options for salmonids in Lake Ontario, for example. Fisheries staff currently stock a mix of salmonids that they feel are desired by anglers and that the lake can produce on a sustained basis. Is the current stocking pattern optimal? The 1988 statewide angler study will permit values analyses that will provide insight into this question.

Risk Assessment and Management

Current research initiatives focus on an assessment of anglers' knowledge of fish consumption advisories, the level of understanding of potential risks involved in consuming Lake Ontario sport fish, and factors influencing participation in contaminated fisheries. One study, funded in part by New York Sea Grant and focusing on Oswego County in New York, addresses public understanding of and compliance with health advisories, and is designed to enable the development of more effective Cooperative Extension communication efforts regarding risks (C. Bisogni, Cornell University, Ithaca, NY, personal communication).

A second initiative, also supported by New York Sea Grant and conducted by one of the authors (Knuth), describes the factors in risk communications information that most influence the ways in which sport fish contaminant risk is viewed by anglers. Another major component of this ongoing study is the inclusion of fisheries and health agency personnel and decision makers to allow comparison of risk perception processes among this group, and between agency personnel and the angling public.

A third initiative, being conducted by the authors (Brown and Knuth), is to be included with the study of calendar 1988 fishing statewide in New York. Emphasis in this survey will be on determining the extent to which anglers are aware of the issued fish consumption advisories for Lake Ontario waters, and the extent to which they follow those recommendations. Without such information, current risk communication strategies cannot be evaluated properly. This information will help managers improve the advisories. The presumption that anglers voluntarily choose to take risks associated with sport fish consumption can be valid only if anglers are aware of and understand the information available regarding health risks and behavioral changes that will help reduce those risks.

Acknowledgements

This research was supported in part through Hatch Project No. NYC-147409, USDA, and by the New York Sea Grant Institute.

References

ARCHER, B. H. 1976. The uses and abuses of multipliers, p. 115–132. *In* C. Gearing, W. Swart, and T. Var [ed.] Planning for tourism development: quantitative approaches. Prager, New York, NY.

BRO, K. M., W. C. SONZOGNI, AND M. E. HANSON. 1987. Relative cancer risks of chemical contaminants in the Great Lakes. Environ. Manage. 11: 495–505.

BROWN, T. L. ca. 1973. The 1973 New York statewide angler survey. N.Y. State Dep. Conserv. Bur. Fish. Rep. 117 p.

1976a. The 1973–75 salmon runs: New York's Salmon River sport fishery, angler activity, and economic impact. N.Y. Sea Grant Inst. Rep. NYSSGP-RS-76-025: 25 p.

1976b. After the ban. Coastlines 7(6): 2.

1977. Economic impact of New York's Great Lakes sport fisheries. J. Great Lakes Res. 3(1–2): 164–166.

ca. 1982. A market segmentation of New York's Great Lakes anglers. N.Y. Sea Grant Inst. Res. Rep. 46 p.

1982. A valuation of New York's Great Lakes sport fisheries. N.Y. Sea Grant Inst. Res. Rep. 24 p.

CONNELLY, N. A., AND T. L. BROWN. 1988. The impact of tourism on employment in New York's coastal areas. Cornell Univ. Dep. Nat. Resour. Res. Extension Ser. No. 32: 58 p.

COX, C., A. VAILLANCOURT, AND A. F. JOHNSON. 1987. A comparison of the results from the "Guide to Eating Ontario Sports Fish" questionnaires. Ontario Ministry of the Environment, Water Resources Branch, Toronto, Ont.

CROUCH, E., AND R. WILSON. 1979. Interspecies comparison of carcinogenic potency, J. Toxicol. Environ. Health 5: 1095–1118.

DAWSON, C. P. 1986. Expenditures of anglers in New York's Great Lakes waters. N.Y. Sea Grant Coop. Extension Publ. 8 p.

DEPARTMENT OF ENVIRONMENTAL CONSERVATION. 1985. Final environmental impact statement for policy on contaminants in fish. New York State Department of Environmental Conservation, Bureau of Environmental Protection, Albany, NY. 150 p.

KRETSER, W. A., AND L. E. KLATT. 1981. 1976–77 New York angler survey final report. New York State Department of Environmental Conservation, Survey and Inventory Unit, Albany, NY. 214 p.

KRUEGER, C. C., D. J. DECKER, AND T. A. GAVIN. 1986. A concept of natural resource management. Trans. Northeast. Sect. Wildl. Soc. p. 50–56.

LAKE ONTARIO COMMITTEE. 1987. Minutes of the Lake Ontario Committee, 1987 Annual Meeting. Great Lakes Fishery Commission, Ann Arbor, MI. 764 p.

LAKE ONTARIO TOXICS COMMITTEE. 1988. DRAFT Lake Ontario toxics management plan. Lake Ontario Toxics Committee, New York State Department of Environmental Conservation, Albany, NY. 46 p. plus appendices.

MARTIN, L. R. G. 1987. Economic impact analysis of a sport fishery on Lake Ontario: an appraisal of method. Trans. Am. Fish. Soc. 116: 461–468.

MENZ, F. C., AND D. P. WILTON. 1983. An economic evaluation of the St. Lawrence River – Eastern Lake Ontario bass fishery. Fish. Bull. 81: 168–175.

MINISTRY OF THE ENVIRONMENT. 1987. Guide to eating Ontario sport fish. Ontario Ministry of the Environment, Communications Branch, Toronto, Ont. 297 p.

PARK, C. N., AND R. D. SNEE. 1983. Quantitative risk assessment: state of the art for carcinogenesis. Am. Stat. 37: 427–441.

PTI ENVIRONMENTAL SERVICES. 1987. DRAFT Guidance manual for assessing human health risks from chemically contaminated fish and shellfish. U.S.E.P.A., Office of Marine and Estuarine Protection, Washington, DC.

SAFE DRINKING WATER COMMITTEE. 1980. Drinking water and health. National Research Council. National Academy Press, Washington, DC.

SCHUMAN, S. P., T. L. BROWN, AND M. W. DUTTWEILER. 1979. The roles of research and extension education in the developing Lake Ontario salmonid fishery. Fisheries 4(3): 6–8.

SKINNER, L. C. 1979. The valuation of New York State fisheries. New York State Department of Environmental Conservation, Bureau of Environmental Protection, Albany, NY.

SONZOGNI, W. C. 1987. The risks associated with Great Lakes contaminants. Proc. Coastal Estuarine Pollut. 5: 1771–1772.

SONZOGNI, W. C., AND W. R. SWAIN. 1984. Perspectives on human health concerns from Great Lakes contaminants, P. 1–29. *In* J. O. Nriagu and M. S. Simmons [ed.] Toxic contaminants in the Great Lakes. John Wiley & Sons, New York, 527 p.

WAYNE COUNTY PUBLIC INFORMATION OFFICE. 1988. The 1988 ESLO trout and salmon derby angler survey: a report and summary. Lyons, NY. 8 p.

CORRECTIONS TO RECENT PUBLICATIONS
CORRECTIONS SUR RÉCENTES PUBLICATIONS

VOLUME 45, No. 1 — article by T. A. Jackson: *The mercury problem in recently formed reservoirs of northern Manitoba (Canada): effects of impoundment and other factors on the production of methyl mercury by microorganisms in sediments.*

Page 107: In Table 11, there is a systematic error in the values for the org. C concentrations and N/org. C molar ratios of sediments collected in 1983 because inorganic C was not subtracted from total C; in addition, the N/org. C molar ratio for West Mynarski Lake was incorrectly computed. The corrected values are as follows:

Sampling site	Org. C (mmol/g)	N/org. C molar ratio
Granville Lake	2.16	0.12
East Mynarski Lake	8.37	0.106
Southern Indian Lake		
Long Bay (shallow cove)	2.58	0.094
Long Bay (main basin)	1.25	0.091
South Bay	1.33	0.064
Methyl Bay (flooded forest)	13.4	0.044
Methyl Bay (offshore)	2.58	0.086
Notigi Reservoir		
Rat Lake	1.75	0.082
West Mynarski Lake	8.70	0.108
Central Mynarski Lake	6.45	0.109
Notigi Lake (west basin)	2.87	0.10
Notigi Lake (east basin)	3.21	0.099

The uncorrected org. C values were used in Fig. 7 (p. 1750) of T. A. Jackson (1988. Can. J. Fish. Aquat. Sci. 45: 1744–1757). However, the resulting systematic error is slight, and its effect on the positions of the points with respect to each other is negligible. Consequently, the pattern of variation shown in the diagram remains essentially unchanged, and the inferences based upon it require no revision.

VOLUME 47, No. 1 — article by S. E. Campana, K. C. T. Zwanenburg, and J. N. Smith: *$^{210}Pb/^{226}Ra$ determination of longevity in redfish.*

Page 164: Equation 2 should read as follows:

$$R_{5<t} = \frac{A_{Pb}}{A_{Ra}}(t) = (1 - e^{-\lambda(t-5)}) + R_{t=5}\,(e^{-\lambda(t-5)}).$$

ANNOUNCEMENTS/AVIS

International Produced Water Symposium

February 4–7, 1992
Catamaran Hotel
San Diego, California

Co-sponsored by American Petroleum Institute, Canadian Petroleum Association, E&P Forum, Environment Canada, Department of Fisheries and Oceans (Canada), Gas Research Institute, Indian and Northern Affairs Canada, Interstate Oil Compact Commission, National Energy Board (Canada), U.S. Department of Energy, U.S. Department of the Interior, Bureau of Land Management, and U.S. Department of the Interior, Minerals Management Service.

The objective of this Symposium is to provide a forum for the presentation and publication of peer-reviewed research results and case studies related to the characterization, treatment, disposal, and environmental fate and effects of produced waters associated with the production of oil and gas.

Approximately 30–50 papers are being sought on a wide range of scientific and engineering topics associated with environmental management of produced waters from the Arctic to the tropics from onshore, coastal, and offshore environments. These topics include, but are not restricted to, the following:

- Characterization and Toxicity Testing (metals, BOD, organics, corrosivity/salinity, radionuclides)
- Fate of Produced Water Discharges and Injected Fluids (monitoring, field studies, dispersion modelling, bioaccumulation, mechanical integrity testing, migration of injected fluids, injection well logging, chemicals to enhance production, corrosion inhibitors, fate and transport)
- Effects (environmental and human health, risk assessment, exposure pathways, air emissions)
- Analytical Methods Development
- New and Proven Technologies for the Treatment, Handling, and Disposal of Produced Water (treatment efficiencies, costs and performance, alternative practices, adaptation of existing methods to new problems, application of new methods, produced sand, beneficial uses, toxicity reduction)
- Waste Minimization and Pollution Prevention (toxic material substitution, chemical treatment and stabilization, source reduction, recycling and beneficial use)

For further information, contact 1992 IPWS, 655 15th Street, N.W., Suite 300, Washington, DC 20005, USA. Telephone: (202) 639-4396; FAX (202) 347-6109.

(English is the official language of the Symposium)

Symposium international sur les eaux de gisement

4–7 février 1992
Hôtel Catamaran
San Diego (Californie)

Le Symposium est parrainé conjointement par le American Petroleum Institute, l'Association pétrolière du Canada, le Forum E&P, Environnement Canada, le ministère des Pêches et des Océans (Canada), le Gas Research Institute, le ministère des Affaires indiennes et du Nord Canada, le Interstate Oil Compact Commission, l'Office national de l'énergie (Canada), le U.S. Department of Energy, le U.S. Department of the Interior, Bureau of Land Management, et le U.S. Department of the Interior, Minerals Management Service.

Ce Symposium a pour objectif d'offrir une tribune pour la présentation et la publication de résultats de recherches reconnus et d'études de cas concernant la caractérisation, le traitement, l'élimination, le devenir environnemental et les effets des eaux de gisement provenant de la production de pétrole et de gaz.

On prévoit environ 30 à 50 présentations portant sur une vaste gamme de sujets scientifiques et techniques liés à la gestion environnementale des eaux de gisement, de l'arctique aux tropiques, dans des milieux terrestres, littoraux et océaniques. Ces sujets touchent, de façon non restrictive, aux domaines suivants :

- Caractérisation et analyse de la toxicité (métaux, DBO, composés organiques, corrosivité/salinité, radionucléides)
- Devenir des rejets d'eau de gisement et de fluides injectés (surveillance, études sur le terrain, modélisation de la dispersion, bioaccumulation, mise à l'essai de l'intégrité mécanique, migration des fluides injectés, diagraphie par injection, emploi de produits chimiques pour améliorer la production, inhibiteurs de corrosion, devenir et transport)
- Effets (milieu naturel et santé publique, évaluation des risques, voies d'exposition, émissions atmosphériques)
- Élaboration de méthodes d'analyse
- Technologies nouvelles et confirmées pour le traitement, la manutention et l'élimination des eaux de gisement (efficacité, coût et rendement du traitement, autres méthodes, adaptation des méthodes existantes aux problèmes nouveaux, application de nouvelles méthodes, sable de gisement, emplois utiles, réduction de la toxicité)
- Limitation des déchets et prévention de la pollution (remplacement des matières toxiques, traitement chimique et stabilisation, réduction de la production à la source, recyclage et emplois utiles)

Pour tout renseignement complémentaire, s'adresser à : 1992 IPWS, 655 15th Street, N.W., Suite 300, Washington, DC 20005, USA. Téléphone : (202) 639-4396; télécopieur : (202) 347-6109.

(L'anglais est la langue officielle du Symposium)

Suns, K., G. Hitchin, and E. Adamek. Present status and temporal trends of organochlorine contaminants in young-of-the-year spottail shiner (*Notropis hudsonius*) from Lake Ontario **1568–1573**
Hartig, J. H., J. F. Kitchell, D. Scavia, and S. B. Brandt. Rehabilitation of Lake Ontario: the role of nutrient reduction and food web dynamics **1574–1580**
Smith, P. G. R., V. Glooschenko, and D. A. Hagan. Coastal wetlands of three Canadian Great Lakes: inventory, current conservation initiatives, and patterns of variation **1581–1594**
Brown, T. L., B. A. Knuth, and F. C. Menz. Lake Ontario's sport fisheries: socioeconomic research progress and needs **1595–1601**

Corrections to recent publications/Corrections sur récentes publications **1602**
Announcements/Avis **1603**

Canadian Journal of Fisheries and Aquatic Sciences

Journal canadien des sciences halieutiques et aquatiques

Volume 48, No. 8, August 1991 — Volume 48, nº 8, août 1991

Frank, K. T. Predicting recruitment variation from year class specific vertebral counts: an analysis of the potential and a plan for verification 1350–1357

Jenkins, G. P., J. W. Young, and T. L. O. Davis. Density dependence of larval growth of a marine fish, the southern bluefin tuna, *Thunnus maccoyii* 1358–1363

Heggenes, J., T. G. Northcote, and A. Peter. Seasonal habitat selection and preferences by cutthroat trout (*Oncorhynchus clarki*) in a small, coastal stream 1364–1370

Munkittrick, K. R., C. B. Portt, G. J. Van Der Kraak, I. R. Smith, and D. A. Rokosh. Impact of bleached kraft mill effluent on population characteristics, liver MFO activity, and serum steroid levels of a Lake Superior white sucker (*Catostomus commersoni*) population 1371–1380

Griffiths, R. W., D. W. Schloesser, J. H. Leach, and W. P. Kovalak. Distribution and dispersal of the zebra mussel (*Dreissena polymorpha*) in the Great Lakes region 1381–1388

Strayer, D. L. Projected distribution of the zebra mussel, *Dreissena polymorpha*, in North America 1389–1395

White, B. A., and J. B. Shaklee. Need for replicated electrophoretic analyses in multiagency genetic stock identification (GSI) programs: examples from a pink salmon (*Oncorhynchus gorbuscha*) GSI fisheries study 1396–1407

Danzmann, R. G., D. S. MacLennan, D. G. Hector, P. D. N. Hebert, and J. Kolasa. Acute and final temperature preferenda as predictors of Lake St. Clair fish catchability 1408–1418

Matsakis, S., and R. J. Conover. Abundance and feeding of Medusae and their potential impact as predators on other zooplankton in Bedford Basin (Nova Scotia, Canada) during spring 1419–1430

Restrepo, V. R., and R. A. Watson. An approach to modeling crustacean egg-bearing fractions as a function of size and season 1431–1436

Hammar, J., J. B. Dempson, and E. Verspoor. Natural hybridization between Arctic char (*Salvelinus alpinus*) and brook trout (*S. fontinalis*): evidence from northern Labrador 1437–1445

Trippel, E. A., and H. H. Harvey. Comparison of methods used to estimate age and length of fishes at sexual maturity using populations of white sucker (*Catostomus commersoni*) 1446–1459

Klotz, R. L. Cycling of phosphatase hydrolyzable phosphorus in streams 1460–1467

Johnston, T. A., R. A. Bodaly, and J. A. Mathias. Predicting fish mercury levels from physical characteristics of boreal reservoirs 1468–1475

Harvey, B. C. Interaction of abiotic and biotic factors influences larval fish survival in an Oklahoma stream 1476–1480

Hare, L., A. Tessier, and P. G. C. Campbell. Trace element distributions in aquatic insects: variations among genera, elements, and lakes 1481–1491

Madenjian, C. P. Limits to growth of young-of-the-year walleye (*Stizostedion vitreum vitreum*): an individual-based model perspective 1492–1499

DePinto, J. V. State of the Lake Ontario ecosystem: introduction to an ecosystem perspective on a vital resource 1500–1502

Martini, I. P., and J. R. Bowlby. Geology of the Lake Ontario basin: a review and outlook 1503–1516

Boyce, F. M., W. M. Schertzer, P. F. Hamblin, and C. R. Murthy. Physical behaviour of Lake Ontario with reference to contaminant pathways and climate change 1517–1528

Schelske, C. L. Historical nutrient enrichment of Lake Ontario: paleolimnological evidence 1529–1538

Crowder, A., and D. S. Painter. Submerged macrophytes in Lake Ontario: current knowledge, importance, threats to stability, and needed studies 1539–1545

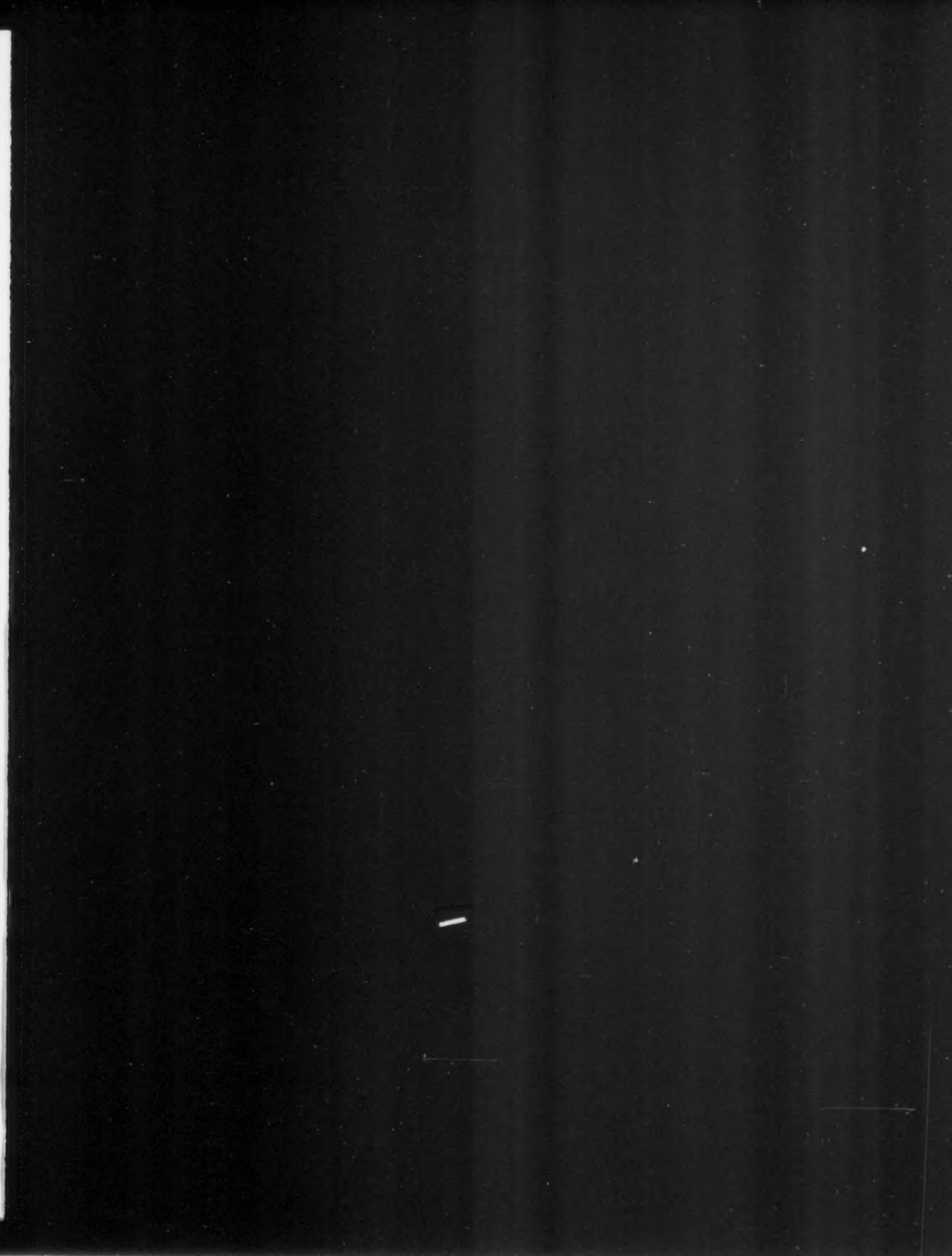
Johannsson, O. E., E. L. Mills, and R. O'Gorman. Changes in the nearshore and offshore zooplankton communities in Lake Ontario: 1981–88 1546–1557

Nalepa, T. F. Status and trends of the Lake Ontario macrobenthos 1558–1567

(Continued inside back)

© Minister of Supply and Services Canada 1991
Ministre des Approvisionnements et Services Canada 1991

CJFSDX48(8) 1349–1603 (1991)
ISSN 0706-652X

Subscription rates/Abonnements

Canada: Institutional/Collectif $210; Personal/Personnel $85
Other countries/Autres pays : Institutional/Collectif $252(U.S.); Personal/Personnel $102(U.S.)
Single issue/Par numéro : $14.95 (Canada); $17.95(U.S.) (Other countries/Autres pays)